Parent-nestling vocal interactions in the white-browed scrubwren

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Declaration

The research described in this thesis is my own work and no part has been submitted for a previous degree. Chapters two, three and four are co-authored by Robert Magrath who contributed discussion of ideas, together with facilities, financial support, some parts of the field work and comments on drafts of manuscripts. All experiments and sound recordings described in this thesis were done exclusively by me and I am the principal contributor to all aspects of the work.

Signed

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Abstract

In this thesis I describe the results of a study on the effects of adult white-browed scrubwren, *Sericornis frontalis*, alarm calls on the behaviour of nestlings and the use of adult provisioning calls during feeding visits.

Evolutionary models and empirical studies imply that nestling begging signals can attract predators and that begging displays are costly. However, parents might reduce or abolish this cost by warning young of the presence of danger. I tested in a controlled field playback experiment whether alarm calls cause scrubwren nestlings to suppress their vocalizations. Nestlings suppressed non-begging vocalization almost completely but only slightly reduced begging calls during a playback of parental feeding calls that followed. The results show that parents can warn young from a distance about the presence of danger and so suppress non-begging vocalizations that might otherwise be overheard, and a parent's presence at the nest presumably indicates when it is safe to beg.

Alarm calls can contain information about the type of predator and the degree of danger. I tested whether scubwren nestlings can distinguish between parental aerial and ground alarm calls and whether their response is adapted to the predation risk of their developmental stage. In a field playback experiment I presented aerial and ground alarm calls, each in a shorter (less urgent) and longer (more urgent) form. Nestlings responded to ground alarm calls by inhibiting their calls, and did so more strongly to the more urgent playback. By contrast, the response to aerial alarm calls started to develop only towards the end of the nestling stage. Thus, scrubwren nestlings can distinguish between different types of alarm calls and react more strongly to calls warning of a predator posing greater danger, in accord with their age-dependent risk.

Dynamic changes in call structure can act as a behavioural response to manage costs and benefits of continued signalling in the presence of a predator. I tested whether scrubwren nestlings use dynamic changes in call structure as a behavioural response to parental alarm calls. Nestlings responded to aerial and ground alarm calls with an increase in frequency and a change in length of their non-begging calls that may lead to a reduction in detectability and localizability. Dynamic changes in call structure are potentially used to optimize the trade-off between the benefits of continuous signalling and the costs of predation. In contrast to non-begging calls, nestlings did not change the

structure of their begging vocalizations, supporting the finding that the presence of an adult acts as an 'all clear' signal.

The use of provisioning calls has been described in a variety of altricial and precocial bird species and their main function is thought to be the stimulation of unresponsive nestlings, especially in the first days after hatching. If this is correct, signal design would only be subject to limited constraints, and indeed the provisioning calls of several species have been described as structurally simple. No current hypothesis can explain a very high level of signal complexity or diversity. Here I describe scrubwren provisioning calls and present data from sound recordings of feeding visits over three consecutive seasons. Adults use provisioning calls that have an extremely high level of structural complexity and comprise a large number of distinct call elements. Despite the high grade of complexity, adults use the calls during feeding visits in ways similar to other species that use structurally simpler calls. Call rates go down as nestlings get older and learn to use other cues to identify a landing adult, and calling behaviour depends on the nestlings' begging response. Although these results suggest that scrubwrens use provisioning calls to stimulate unresponsive nestlings, the extreme signal complexity indicates that other functions might be relevant.

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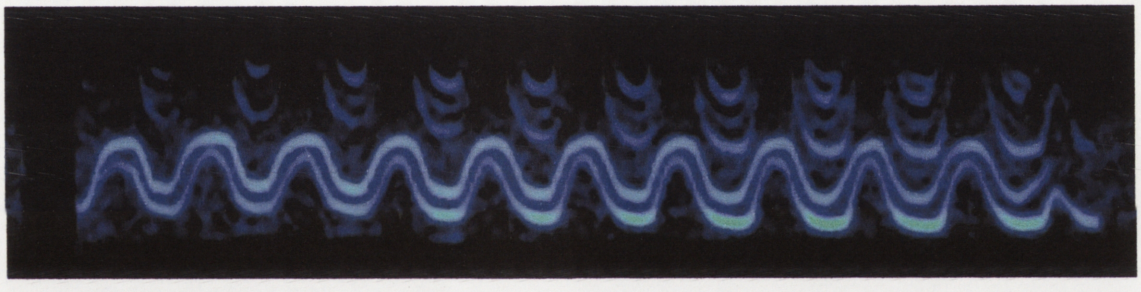
General introduction

Chapter 1



(white-browed scrubwren provisioning call)

This thesis deals with the communication between adults and nestlings of the white-browed scrubwren, *Sercornis frontalis*. I focus in particular on adult alarm and provisioning calls and their effect on the behaviour of scrubwren nestlings. Utilizing field playback experiments I analyze how nestlings change their calling activity and call structure in response to adult alarm calls. With I also describe how adults use provisioning calls to stimulate nestlings and how the nestlings' response influences the adults' calling activity. All four data chapters of this thesis deal with a specific topic and are written in a manuscript style. Consequently, I review the relevant literature in the introduction to each chapter rather than in this general introduction. Similarly I discuss all results in detail at the end of each chapter instead of in a general discussion. In this general introduction I will provide a brief conceptual overview of the questions raised in the following chapters and outline the structure of the thesis.

The vocal interactions between adult birds and their young have gained considerable attention within the last decade, although almost exclusively in the form of signalling nestlings and receiving parents (Budden & Wright 2001; Wright & Leonard 2002). The feeding visits of adults are in many bird species accompanied by loud and extravagant begging signals from their young that transfer information on hunger state, condition and health to the feeding adults (Kilner 2002; Sacchi et al. 2002; Wright & Leonard 2002; Saino et al. 2003). More intense begging is often related to hunger and leads to an increase of parental provisioning (Budden & Wright 2001). For a long time it has been thought that these signals must be costly in terms of energy expenditure and possible attraction of predators (Godfray 1995). Costs associated with exaggerated begging could prevent nestlings from signalling dishonestly to increase the amount of food distributed to them (Kilner & Johnstone 1997). The energetic costs of begging displays have been shown to be low and are unlikely to prevent dishonest signalling (Chappell & Bachman 2002), but the role of predation is less clear.

Nest predation is potentially a major cost, but reliable estimates of actual costs caused by nestling begging are difficult to get, and it is still unclear whether predation is a factor that can prevent dishonest signalling (Haskell 2002). Most studies so far have overlooked that parental behaviour can influence the predation costs related to begging. Parental alarm calls can potentially warn nestlings of a predator that is close enough to the nest to overhear the begging calls (Ryden 1978a; Greig-Smith 1980). In the first part of my thesis I present the results of two field playback experiments that I conducted to

answer the question of whether nestlings respond to parental alarm calls with a suppression of begging activity.

1. Alarm calls

(a) Alarm calls and nestling vocalizations

The loudness and intensity of nestling begging in many bird species has led to the idea that these signals are costly because they can attract predators (Haskell 2002). Although intuitive, this theory is difficult to prove empirically. Several across-species comparisons have indicated that the structure of begging signals varies with predation risk and that species with high predation risks have less conspicuous calls (Redondo & De Reyna 1988; Popp & Ficken 1991; Briskie et al. 1999). The results of these studies are difficult to interpret because they do not take into account that nest predation can be influenced by a variety of factors. Nest site, parental activity and nestling activity all affect the likelihood of predation (Martin et al. 2000). The predation costs that are actually caused by the nestling begging signals have to be separated from costs caused by other factors, and are likely to represent only a part of the overall probability of nest predation (Haskell 2002).

To avoid confounding parental as well as nest-site effects several studies have used artificial clutches and nests in combination with playbacks of nestling vocalizations (Haskell 1994; Leech & Leonard 1997; Dearborn 1999; Haskell 1999). The results of these studies have shown that potential nest predators can be attracted to nests. However, artificial nests and nest sites have unpredictable side effects (Major & Kendal 1996) and it is often uncertain whether the attracted predators are relevant nest predators. Furthermore, parental effects could have an increasing or decreasing effect on nest predation. Although it has been generally assumed that parental activity at the nest increases nest predation (Martin et al. 2000), parents can potentially decrease negative effects of nestling vocalization by warning their young when a predator is nearby.

The evidence that nestlings respond to parental alarm calls is inconclusive. Several laboratory and field studies have suggested that nestlings reduce begging when presented with adult alarm calls but most of the alarm calls used in experiments were pseudoreplicated and the experiments lacked appropriate controls (Ryden 1978b; Greig-Smith 1980; Knight & Temple 1986). A recent laboratory study on white-browed scrubwrens that used controlled and replicated playbacks showed that nestlings

responded to parental alarm calls with increased vocalization (Maurer et al. 2003). I conducted a controlled playback experiment at scrubwren nests to answer the question of whether nestlings respond to parental alarm calls in the field. The results of this study are the subject of chapter 2.

(b) Development of the alarm call response

It was first demonstrated in primates that structurally different alarm calls can be used by animals to refer to different types of threat and that receivers use the different alarm calls to respond adaptively (Seyfarth & Cheney 1980). Many rodent species potentially encode information about the urgency of a threat in their alarm calls (Macedonia & Evans 1993). The alarm calls of birds show structural differences between calls that warn of aerial predators and calls that are given when a predator moves on the ground (Marler 1957). It thus seems likely that these calls refer to a certain type of predator, but this has only been formally shown in the domestic fowl, *Gallus gallus* (Evans et al. 1993). The use of alarm calls that contain information on the urgency of a threat has been demonstrated only for the aerial alarm calls of white-browed scrubwrens that use longer alarm calls in more urgent situations (Leavesley & Magrath in press). No study to date has tested whether nestlings distinguish between the different types of alarm calls and respond accordingly.

It is vital for the young of many species to respond correctly to adult alarm calls because their flight response is not fully developed (Mateo 1996). A distinction between different types of alarm calls seems relevant if the predators the calls warn of pose a different threat to the young and require different responses. Hanson and Coss (1997; 2001) showed that the young of California ground squirrels, *Spermophilus beecheyi*, respond more strongly to ground than aerial alarm calls. This is the opposite response of what is found in adults, where aerial alarm calls lead to a stronger flight response. One possible explanation for the difference is that juveniles are vulnerable to different predators compared to adults, and that they respond according to their age-dependent risk (Owings & Loughry 1985). This concept might also apply to the development of birds (Miller & Hicinbothom 1991). Surprisingly this has never been formally tested, although the threat from aerial and ground predators is likely to be different for nestlings compared to fledglings and adults. I conducted the experiment that is outlined in chapter 2 to test whether scubwren nestlings respond differently to aerial and ground alarm calls and whether their response is in agreement with their age-dependent risk.

(c) Structural changes of nestling calls in response to alarm calls

The most common response to the detection of a predator is an inhibition of any calling activity (Zuk & Kolluru 1998). Another possible response is to keep calling, but change the structure of the calls in a way that makes them harder for the predator to detect (Bayly & Evans 2003). These dynamic changes in signal design represent a short-term adaptation to predation threat that potentially enables an individual to negotiate the trade-off between signal costs and benefits. The attraction calls of male Tungara frogs, *Physalaemus pustulosus* (Ryan et al. 1982), exemplify both principles. The calls consist of high frequency and low frequency components and are used by males to attract females. The low frequency components enable females to assess the males' body size and are more attractive to them than the high frequency components. However, predatory bats can cue in on the low frequency components and successfully hunt males that use them (Ryan et al. 1983). Males have two ways of avoiding predation by bats. Firstly, they avoid using low frequency components unless a neighbouring male starts calling and they are in danger of loosing a mating opportunity. Secondly, they leave the low frequency components out when they detect a bat nearby. The selective inhibition of call elements effectively changes the frequencies of the used calls in a way that reduces the danger of being depredated while calling.

Dynamic changes of signal structure have been shown in the aerial alarm calls of several bird species. Domestic fowl reduce the low frequency introductory components of their call elements throughout a call bout to avoid detection by the predator (Bayly & Evans 2003). White-browed scrubwrens increase the minimum frequencies of calls in situations of higher threat (Leavesley & Magrath in press), and similar changes have been observed in chickadees (Ficken 1990). It seems likely that dynamic changes in signal structure in response to threat are more common in songbirds than these examples suggest, due to their exceptional control over sound production (Gaunt & Nowicki 1998). For example it seems possible that nestlings could modify the structure of calls in response to adult alarm calls, rather than falling completely silent. Chapter 3 describes the results of a study that tested for structural changes in calls of scrubwren nestlings that kept on calling after hearing alarm calls.

2. Provisioning calls

The use of acoustic signals by adults during the feeding of young birds has been studied for almost one hundred years (Kuhlmann 1909), and occurs commonly in altricial as well as precocial species (Beer 1970; Buitron & Nuechterlein 1993; Clemmons 1995). Despite the comparatively long history of knowledge about 'provisioning calls', these acoustic signals have hardly ever been subject of a detailed analysis. There is no theoretical framework about their evolutionary context or possible benefits. This is specially surprising because avian acoustic communication in general, and the vocal signals of begging nestlings during feeding events in particular, have attracted a great deal of theoretical as well as empirical research (Kroodsma & Miller 1996; Wright & Leonard 2002).

Arguably the lack of research in this area is due to the perception that provisioning calls are solely used to stimulate nestling begging when nestlings are unresponsive (Bengtsson & Ryden 1981; Khayutin 1985; Clemmons 1995). This theoretical concept implies that nestlings as well as adults benefit from the signalling process. Together with the lack of environmental constraints on the signal transfer between adults and nestlings (but see Horn & Leonard 2002), this view has promoted the idea that provisioning calls are of simple structure and function. The only factor shaping signal design seems to be a potential cost of predation due to signalling at the nest (Yasukawa 1989; Leonard et al. 1997). This theoretical framework appears to explain the use of provisioning calls in many species, but does not explain the occurrence of signal complexity or diversity in provisioning calls.

The idea that provisioning calls can be used for parent-offspring recognition has been developed in species that show a more complex signal design and individual variation in call structure. Provisioning calls of this form have been found in several species (Sieber 1985; Lessells et al. 1995; Leonard et al. 1997) and can be used by the young to distinguish between adults feeding at their nest and other adults living in the same colony (Sieber 1985; Leonard et al. 1997). Proposed benefits of parent-offspring recognition are a decreased risk of attack by unrelated adults as well as misdirected solicitation by young and misdirected care by adults (Beecher et al. 1985; Searby et al. 2004).

The possibility that adults seek to maximize the amount of information they gather about nestling condition and health by stimulating their brood with provisioning

calls has been mentioned (Bengtsson & Ryden 1981; Leonard et al. 1997), but not formulated as a testable hypothesis. Nestling begging can transfer information about condition, hunger and health (Kilner 2002; Sacchi et al. 2002; Saino et al. 2003). The more information adults get about the current state of their brood the better they can potentially optimize their investment. For example, if only one nestling begs, adults might choose to stimulate other nestlings to beg as well to compare condition and health of their young. Parental control over distribution of food and the preferential feeding of nestlings have been shown in several species (Lessells 2002).

The current ideas on the use and structure of provisioning calls can be formulated as hypotheses with testable predictions:

(1) Facilitation of feeding: This hypothesis states that adults use provisioning calls to make feeding more efficient when nestlings do not respond with begging and gaping to the presence of a parent. This could be necessary because nestlings are too young to respond to the landing noises or to see the adult, or because they have a low begging motivation. The main prediction of this hypothesis is that provisioning calls should not be used when one or more nestlings respond by begging to the arrival of an adult. If nestling responsiveness increases with age, either by learning or maturation of sensory perception, the usage of provisioning calls should decline. The number of calls used in each visit should be low. Signal design can be expected to be simple, as it only needs to stand out from environment noise and give the nestlings a reliable cue for the presence of an adult irrespective of its identity.

(2) Parent-offspring recognition: This hypothesis states that adults use provisioning calls as individual traits to enable identification of parents or helpers by the young. Predictions are that adults use provisioning calls even when nestlings are older and independent of the nestlings' response. The signal design should be complex and diverse enough to allow for a level of individual variation that ensures that adults can be reliably distinguished. Signal design should have high variability on the population level in colonial species, but variability between adults feeding at one nest needs only to be high if brood division occurs. In non-colonial species one of the main reasons for individual recognition seems to be brood division. If the likelihood of encountering strangers in the natal territory is low, signal design should vary between adults feeding at one nest but not necessarily on the population level.

(3) Acquisition of information: This hypothesis states that adults use provisioning calls to stimulate a higher level of begging activity from their nestlings than they would display without the calls. A high level of begging activity potentially transfers a greater amount of information on nestling condition and health, and enables adults to optimize their decision on who to feed. Predictions are that adults should use provisioning calls if nestlings show no or low levels of begging activity, even when nestlings get older. Adults should also call when only one nestling is begging. The number of calls should vary with nestling activity. The signal design should ensure a high level of stimulation of the nestlings but does not need to show high levels of individual variation within a population.

The provisioning call system of the white-browed scrubwren is characterized by several features that potentially cannot be explained by any of the current hypotheses on the use of provisioning calls. Scrubwren provisioning calls show an extremely high degree of structural complexity and constitute the first example of a provisioning call system that consists of a variety of call types. Many of the identified call types originate from species-specific vocalizations, such as song elements, which are given outside of their normal context. Adults also imitate other bird species during feeding visits. They use long calling bouts that contain many call elements and the call structure shows no obvious form of individual variation. Provisioning calls are still used at nests with older nestlings that already respond to stimuli other than adult vocalization.

These findings need to be tested against the already established hypothesis about the use and design of provisioning calls, but potentially require a new theoretical framework about the benefits of provisioning calls.

3. Thesis outline

Chapter 2

This chapter describes the results of a field playback experiment in which I tested whether nestlings responded to adult alarm calls by suppressing their vocalizations. Nestling scrubwrens use non-begging as well as begging vocalizations and I tested the effect of adult ground alarm calls on both types of vocalization. Nestlings responded to the playbacks by suppressing their non-begging vocalizations much more strongly than their begging vocalizations. The implications of the results for the theories on the evolution of begging vocalizations are discussed.

Chapter 3

To test whether the nestlings can distinguish between different types of alarm calls I conducted an experiment that tested aerial as well as ground alarm calls in a longer (urgent) and shorter (less urgent) form. This chapter describes the effects on the nestlings' non-begging vocalizations. Nestlings distinguished between the two types of alarm calls and used the length of the ground alarm calls to adjust their response strength. These results support the hypothesis that nestlings respond to alarm calls according to their age-dependent risk.

Chapter 4

I tested whether nestlings respond to alarm calls with dynamic changes in signal design as well as vocal inhibition. I analyzed the call structure of non-begging and begging vocalizations for the same experiment that is described in chapter 2. The results indicate that nestlings change the design of their non-begging but not their begging calls after hearing alarm calls.

Chapter 5

This chapter describes the use and design of scrubwren provisioning calls. I compare the results with the three current hypotheses on the use of provisioning calls and results of studies on other species. I also propose three new hypotheses and compare their predictions with the results of this study.

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Parental alarm calls suppress nestling vocalization

Chapter 2

Platzen, D. & Magrath, R. D. 2004 *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**, 1271-1276.

Evolutionary models suggest that the cost of a signal can ensure its honesty. Empirical studies of nestling begging imply that predator attraction can impose such a cost. However, parents might reduce or abolish this cost by warning young of the presence of danger. We tested in a controlled field playback experiment whether alarm calls cause 5, 8 and 11 day old nestlings of the white-browed scrubwren, *Sericornis frontalis*, to suppress vocalization. In this species, nestlings vocalize when parents visit the nest ("begging"), and also when they are absent ("non-begging"), so we measured effects on both types of vocalizations. Playback of parental alarm calls suppressed non-begging vocalization almost completely but only slightly reduced begging calls during a playback of parental feeding calls that followed. The reaction of nestlings was largely independent of age. Our results suggest two reasons why experiments ignoring the role of parents probably overestimate the real cost of nestling vocalizations. Parents can warn young from a distance about the presence of danger and so suppress non-begging vocalizations that might otherwise be overheard, and a parent's presence at the nest presumably indicates when it is safe to beg.

1. INTRODUCTION

Begging by nestling birds has been used to test evolutionary models of signalling that suggest that the honesty of communication depends on dishonesty being costly (Johnstone & Godfray 2002). Nestlings beg using vocal signals, colourful mouths and postural displays to transfer information about hunger state, size and health (Budden & Wright 2001a). Conflicts of interest between parents and offspring, and among siblings, about the amount and distribution of food could lead to dishonest exaggeration unless it is reigned in by costs (Godfray 1995; Rodriguez-Girones 1999). The two likely costs of exaggeration are increased energy expenditure and risk of predation (Chappell & Bachman 2002; Haskell 2002). The evidence so far suggests that energetic costs are minimal (Chappell & Bachman 2002), although it is possible that they are best measured by growth rather than metabolic rate (Kilner 2001; but see Leonard *et al.* 2003). Here we focus on the potential costs of predation.

Predation is potentially a major cost, but it has proved difficult to gain realistic estimates of the cost (Haskell 2002). Across species comparisons showed that species with high predation rates have begging calls that are probably more difficult to overhear or locate (Redondo & De Reyna 1988; Popp & Ficken 1991; Briskie *et al.* 1999). It is difficult to interpret these results as there is no necessary connection between predation rates and the cost of begging vocalizations. The predation costs of begging are represented only by the share of total nest predation that is directly caused by begging noise, rendering across species comparisons problematic as nest predators and nesting ecology are highly variable (Haskell 2002). Experimental studies avoid these problems and have found that playback of begging calls can attract predators (Haskell 1994, 1999; Dearborn 1999; Leech & Leonard 1997). However, while these results show that predators can hear and respond to begging calls, they do not estimate the actual risks (Haskell 2002). In addition to being carried out at artificial nests or sites, these experiments did not take into account the behaviour of parents. This is an important limitation.

Parents potentially warn young of danger so that they do not vocalize when predators are near. If parents do indeed warn nestlings to keep quiet, it means that playbacks of begging cannot estimate the real risk that predators will overhear nestlings.

So far the evidence that parents can suppress nestling vocalizations is suggestive but incomplete. Early playback studies were performed by Ryden (1978) and Greig-Smith (1980), who showed that great tit, *Parus major*, and stonechat, *Saxicola torquate*, nestlings respectively suppressed begging after hearing alarm call playbacks. In a third study Knight and Temple (1986) observed that nestling American goldfinches, *Carduelis tristis*, crouch into the nest upon hearing alarm call playbacks in the field, but did not analyse nestling vocalisation. These studies are suggestive, but incomplete because they suffer from pseudoreplication of playback stimuli. Halupka (1998) found that nestlings became silent when a human walked near the nest, and suggested that the parents' alarm calls were responsible. However, it is possible that parents warned the nestlings in other ways, or that nestlings detected the human independently of the behaviour of the parent. A study by Kleindorfer *et al.* (1996) had similar limitations. One laboratory experiment on white-browed scrubwrens, *Sericornis frontalis*, showed that adult alarm calls did not suppress nestling vocalizations; in fact, nestlings responded to alarm calls with increased vocalisations (Maurer *et al.* 2003). However, that experiment was possibly constrained by the laboratory environment and requires testing on nestlings in the field. Overall, there is no strong evidence that parental alarm calls suppress nestling vocalizations, despite the plausibility that they do so and the potential for parents to thereby modulate the costs of begging (Haskell 2002).

Here we report the results of a field playback experiment that tested whether parental alarm calls suppress nestling vocalizations. We carried out playbacks to white-browed scrubwren nestlings at three ages. Scrubwren nestlings vocalize not only during feeding visits ('begging'), but also when no adult is near the nest ('non-begging'). We therefore assessed the effect of parental alarm calls on each type of vocalization. Nestlings were tested for their response to parental 'buzz' alarm calls directly, without any other sign of an adult, and subsequently during a playback of adult feeding calls that imitated the arrival of an adult at the nest with food. We predicted that nestlings reduce begging as well as non-begging vocalizations after hearing parental alarm calls.

2. METHODS

(a) Study species

The white-browed scrubwren is a small passerine in the family Acanthizidae (Schodde & Mason 1999) that builds well-hidden domed nests on or near the ground. The mean brood size in scrubwrens is three nestlings and young fledge at about 15 days (Magrath *et al.* 2000). Scrubwrens can breed in pairs or trios, consisting of a dominant pair and subordinate male (Magrath 2001), but we confined our experiments to birds breeding in pairs. The birds were studied in the Australian National Botanic Gardens, Canberra (35°16'S, 149°06'N), and all were colour marked to allow individual recognition.

Depredation of nest contents increases from a consistent 1% per day on eggs to 5% per day within four days of hatching (R. D. Magrath, unpubl.), suggesting that the nestlings, or adults feeding them, betray the nest location. Pied currawongs, *Strepera graculina*, large omnivorous birds, are the major predator of scrubwren nestlings at the study site (Prawiradilaga 1996) and presumably hunt by sight and sound.

Nestlings have two different types of vocalization (Maurer *et al.* 2003). When begging during a feeding visit they give long and loud 'whine' calls with a broad frequency range. In between feeding visits, when parents are absent, they vocalize with a short and soft high pitched 'peep' call. Peeps also often follow whines in the later stages of a feeding visit. Vocalization during the absence of the parents is common and the call rate of a brood can vary from 0 up to 200 calls per minute in the field (D. Platzen, unpubl).

Parents give 'buzz' alarm calls, which are short and of a broad frequency range, when a predator is perched or on the ground close to the nest (Higgins & Peter 2002). This call is normally repeated in rapid succession and a call sequence can last up to several minutes depending on how long the danger is present (D. Platzen, unpubl.). When arriving at the nest with food parents give short "chip" calls and just before feeding long, modulated "provisioning" calls (Higgins & Peter 2002).

(b) Playback experiment

The experiment was designed to test whether a playback of alarm calls suppressed non-begging vocalizations (peeps), and whether begging vocalizations

(whines or peeps) were also suppressed during a playback of chip and provisioning calls shortly after the alarm call playback. The playback sequence consisted of 10 sec of alarm calls, 15 sec of silence and a 3.5 sec long series of the parental feeding calls. Although adults can alarm call for longer than 10 seconds in the wild, we chose this time to avoid interference by parents that might overhear the playback. The period of silence was used to record the non-begging vocalizations and it was designed to be short enough to ensure that any effect of the preceding playbacks was still present at the beginning of the chip and provisioning call playback. The parental feeding vocalizations consisted of four chip calls followed by a provisioning call, which is a common pattern of adult vocalizations given on arrival at the nest with food. The begging response of the nestlings was recorded for 15 sec following the first chip call. In the control playbacks we substituted the alarm calls with 10 seconds of background noise taken from the same recording as the adults' calls, and filtered and amplified in the same way. This control tests whether our experimental procedure, or background sounds recorded along with the adults' vocalizations, affected the nestlings. It is the appropriate control given the question of whether nestlings change their behaviour after hearing their parents' alarm calls, compared to their parents being absent or remaining silent. We did not address the separate issue of what acoustic features of alarms are important.

The playback tapes were prepared with calls from each brood's own parents, and therefore avoided any effects of pseudoreplication (Kroodsma 1998) or parent-offspring recognition (Medvin *et al.* 1992). Alarm calls were obtained when nestlings were 3 or 4 days old by placing a mounted currawong close to the nest on the ground while the parents were foraging. Adults gave buzz alarm calls on their return and these were recorded onto a Sony TCD-D100 DAT recorder at 44.1kHz sampling frequency with an Audio Technica ATM15a condenser lapel microphone attached close to the nest. The recordings were edited and amplified to achieve standardized call rates (6 calls/min) and amplitudes. The adults' chip and provisioning calls were recorded with the same equipment during natural feeding visits, with the microphone 16cm from the nest entrance. Recordings were digitally transferred onto a Macintosh computer, filtered to remove sound below 2kHz, and edited for playback (below) using Canary 1.2.4. (Charif *et al.* 1995).

Experiments were conducted between October and December 2001 at 11 different nests when nestlings were 5, 8 and 11 days old. All experimental broods had three nestlings. We placed an ATM15a microphone 16 cm from the nest entrance,

connected by a 15 m cable to a DAT recorder, and a Sony SRS-A60 active speaker one meter from the nest, connected to another DAT recorder. After 30 to 45 minutes acclimatization, we waited for the adults to be out of our hearing range (≥ 20 m) to avoid the behaviour of the nestlings being influenced by any parental calls or activities, or that the adults overheard our alarm call playbacks. We then played either an alarm call or a control from the speaker while simultaneously recording the nestlings. The second playback series followed at least one natural feeding visit (5 – 20 minutes). The order of alarm and control playbacks was changed from nest to nest but remained the same for one nest on all three tested ages. Habituation or learning effects are extremely unlikely as all calls used in our playbacks occur frequently in the auditory environment of the nestlings. Calls were played back to the nestlings at natural sound levels: buzz calls 45 -55 dB (Mean ± SE of field recordings: 54.3 ± 4.0 dB); chip calls 60 - 70 dB (71.4 ± 4.8 dB); and provisioning calls 45 - 55 dB (53.2 ± 7.5 dB). Background playback was 35 - 40 dB (39.4 ± 3.2 dB) following editing and amplification of alarm calls. Decibel values are re $1pW/m^2$. Recordings were calibrated in Canary using a reference file of known sound pressure level, measured with a Bruel & Kjaer type 2205 sound level meter.

We digitally transferred the recordings of broods to Canary and measured both non-begging vocalizations, in the 15 sec after alarm playback, and begging vocalizations, in the 15 sec after the simulated parental visit, using a filter bandwidth of 699.4 Hz, a grid resolution of 43.07 Hz with 50% overlap. We counted the number of non-begging vocalizations and measured the start time, duration, average amplitude, and minimum, maximum and peak frequency, for every begging vocalization to test for changes in call structure in reaction to our playbacks. We measured overlapping vocalizations when more than one nestling called at a time, but excluded these calls from the amplitude and peak frequency analysis.

(c) Statistical analysis

Despite the experimental design, the data were not fully balanced because two broods were depredated before day 11 (n = 9 on day 11) and technical difficulties at one nest (day 8) as well as adult interference at 4 nests (twice on day 5, once on day 8 and day 11 respectively) led to only partial data sampling for some but not all variables. Furthermore, variables relating to the attributes of begging calls were missing if broods

were silent (day 5 = 1, day 8 = 2, day 11 = 1), so that the sample size varies with analyses.

We analysed non-begging and begging vocalizations separately. (a) *Non-begging vocalizations*: In 24 out of 31 experiments the reaction to alarm calls was silence (day 5, 8 and 11 = 8) so we modelled the probability of vocalising using a Generalized Linear Mixed Model with restricted maximum likelihood estimation (REML) in Genstat 5 (release 4.2, Genstat-Committee 2000). Fixed effects were type of playback (alarm or control), age of nestlings, daytime, and an interaction term of age and type of playback. Brood identification was used as a random factor. We used Wald statistics to assess the significance of fixed effects when the effect of interest was last in the model (Genstat-Committee 2000). (b) *Begging vocalizations*: We used a Linear Mixed Model with REML estimation with the same random and fixed effects as in the "non-begging" analysis. To assess significance, we calculated the change in deviance caused by dropping the fixed effect of interest with the sub-model routine implemented in Genstat (Genstat-Committee 2000). As well as the call features already described we used the time from the start of the playback to the beginning of the first nestling call as a measure of response latency. We transformed this variable with a natural logarithm to normalize the residuals. The residuals of all other models did not deviate from normality.

3. RESULTS

(a) Reaction to alarm calls

Broods went completely silent after playback of alarm calls, but not control sounds, in almost all experiments (alarm vs control: $\chi^2_1 = 21.5, p < 0.001$; figure 1a). No other variable had a significant influence on nestling vocalization (age: $\chi^2_2 = 0.1$, $p = 0.93$, daytime: $\chi^2_2 = 0.3$, $p = 0.77$, age*playback: $\chi^2_2 = 0.5$, $p = 0.61$). Furthermore, even in the 7/31 experiments in which the brood did not go silent, the average number of calls was lower after the alarm playback compared to the control (two tailed exact test: $p = 0.047$; figure 1b). Only in one of these experiments was the number of calls after the alarm calls higher than after the control (4 calls compared to 1).

(b) Reaction to chip and provisioning calls

Nestlings begged less vigorously to simulated parental visits after hearing alarm calls than after hearing the control playback. The latency of the response increased ($\chi^2_1 = 9.0$, $p = 0.003$; figure 2a) and the total duration of all calls decreased after the alarm call playback ($\chi^2_1 = 5.2$, $p = 0.022$; figure 2b). The frequencies of the calls given by nestlings did not change significantly although there was a trend towards an increase in low frequencies following alarm calls (low frequency: $\chi^2_1 = 3.5$, $p = 0.06$; high frequency: $\chi^2_1 = 0.3$, $p = 0.8$; peak frequency: $\chi^2_1 = 1.0$, $p = 0.33$). Young nestlings did not change the amplitude of their calls according to playback type, but 11 day old nestlings begged more quietly after the alarm than control playback (playback*age: $\chi^2_2 = 6.3$, $p = 0.043$; figure 3).

4. DISCUSSION

Parental alarm calls almost completely suppressed non-begging nestling calls and reduced begging calls during a simulated feeding visit. This is the first robust evidence that adult alarm calls can transfer information about the presence of danger to nestlings. Given that parental alarms can suppress nestling vocalization, it follows that playback experiments that use artificial nests are likely to exaggerate the true likelihood of predation and therefore cost of vocalising.

Although alarm calls almost completely suppressed non-begging vocalization, they caused only a 30% reduction in the duration of begging vocalization compared to the control playbacks. Furthermore, we found no effect of preceding alarm calls on call frequencies and no uniform reduction of amplitude (below). We suggest that the much greater effect on non-begging vocalization is adaptive because the arrival of a parent at the nest is an "all clear" signal indicating that danger has passed. Adults appear cautious when approaching the nest with food, and so seem unlikely to overlook predators within earshot of the brood. Furthermore, it is even less likely that they would feed young in the presence of a predator that has already prompted alarm calls, or overlook another predator in these circumstances. Our results imply that the cost of begging due to predation risk is likely to be small, and that evolutionary models that assume low costs of begging activity may be relevant. These could either be cost-free honest signalling models (Maynard Smith 1994; Bergstrom & Lachmann 1998), different theoretical approaches that focus on begging as a consequence of sibling competition, or signalling of information other than nestling need (e.g. health Saino *et al.* 2000). Our results suggest that costly signalling in the white-browed scrubwren occurs in the absence of parents rather than in their presence.

If begging calls are usually only given after the 'all clear' signals of an arriving parent, then predators may have little opportunity to overhear these calls, and it is more relevant to examine the likelihood of predators overhearing vocalizations given when parents are not at the nest. There has been relatively little study of vocalizations in the absence of parents (Greig-Smith 1980; Wright & Cuthill 1990; Budden & Wright 2001b; Leonard & Horn 2001b; Roulin 2002). In some species, at least, the calls resemble those given when parents are present, and so could be "mistaken" begging in response to other stimuli, in which case such calls could be considered a "cost of begging" (Leonard & Horn 2001b). In the scrubwren, however, these non-begging

vocalizations (peeps) are quite different from begging calls (whines), suggesting they are not mistakes and that any costs to peeps could be independent of the cost of begging. The adaptive significance of these signals remains to be tested. The acoustic structure of scrubwren peeps, which are narrow-band, short calls, compared to whines, implies that they may have evolved to be difficult for predators to overhear or locate (Klump 2000). Nonetheless, as they are given over a long period of time, they still might be overheard by a predator that comes close enough to the nest. By contrast, the broad-band, long nature of whine calls suggest that begging vocalizations have been subject to little selection from predation, consistent with parental arrival acting as an "all clear" signal.

Our results contrast with a previous laboratory study on scrubwrens by Maurer *et al.* (2003), who found that playback of adult alarm calls increased nestling calls and did not affect begging vocalizations during simulated parental visits. Possible causes of the contrasting results are (1) that we used the parent's own vocalizations during playbacks, whereas Maurer *et al.* (2003) were constrained to use calls from strangers, and (2) that we used the responses of whole broods in their natural nests, whereas Maurer *et al.* (2003) isolated individual nestlings. Other studies of isolated nestlings imply natural behaviour (Greig-Smith 1980; Leonard & Horn 2001a), although we know of no explicit tests of the effects of isolation. Maurer *et al.* (2003) suggested that the paradoxical behaviour of nestlings may have been the result of developmental constraints, and studies of other species have reported an increase in responsiveness to alarm calls in later ages (Khayutin 1985; Kleindorfer *et al.* 1996). However, we found only minor age effects, despite testing nestlings up to 11 days old, only 4 days before the mean fledging age.

We conclude that parent-offspring communication about predators must be included in evolutionary models of begging and taken into account in further empirical studies. We also urge study of the function and costs of non-begging vocalization, which seem more likely to suffer the cost of increased predation despite being more difficult to overhear. By contrast, most studies have focused almost exclusively on begging in the presence of parents, which could be almost exempt from such costs.

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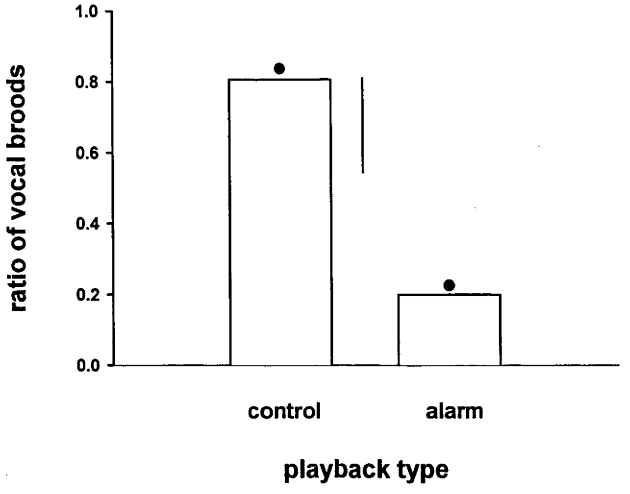

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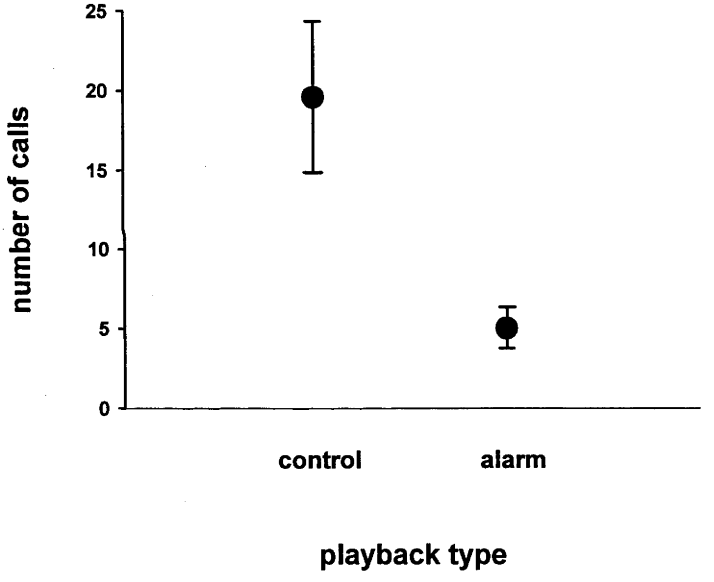
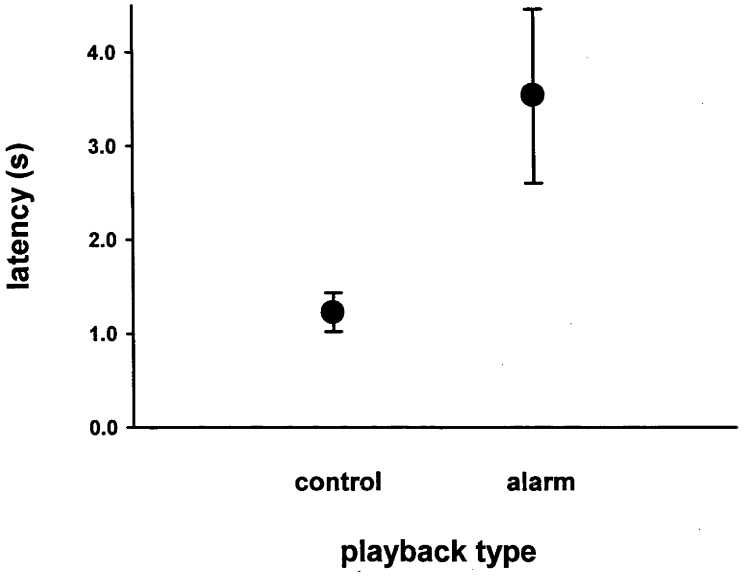


Figure 1: Reaction to alarm calls. (a) Ratio of broods that kept vocalizing during the 15 second interval after the experimental playbacks. Bars show means estimated from a mixed model, the line between the bars represents the least significant difference, and the black dots represent means of the observed data. (b) Number of calls that were given by the 7 broods in which nestlings kept vocalizing after control as well as alarm call playbacks. Means and standard errors are depicted.

a)



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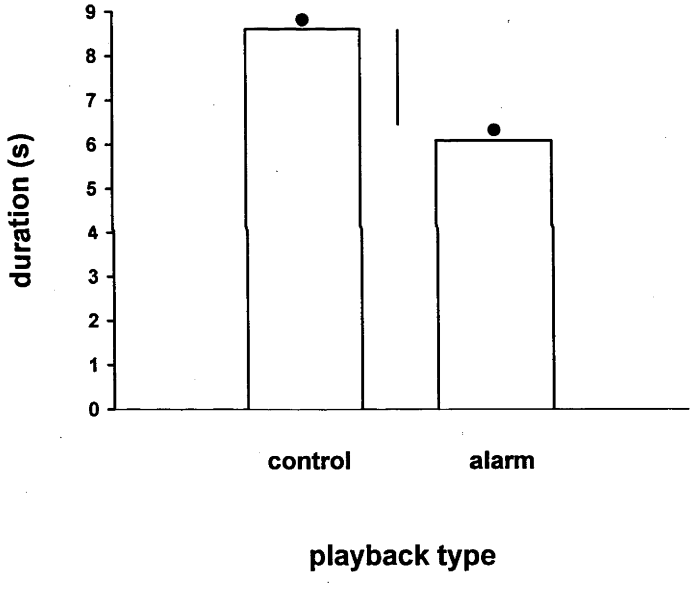

Figure 2: Begging response to the chip and provisioning calls. (a) Latency until nestlings start to call (mean ± s.e.m.). (b) Total duration of all calls. Bars show means estimated from a mixed model, the line between the bars represents the least significant difference, and the black dots represent means of the observed data.

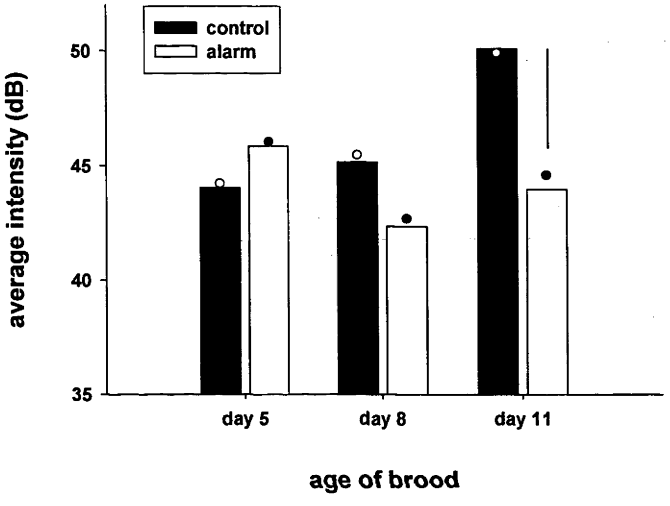

Figure 3: Amplitude of the begging response. Bars show means for control (filled bars) and alarm (open bars) playbacks estimated from a mixed model over the three age classes, the line between the two last bars represents the least significant difference, and the black and white dots represent means of the observed data.

Adaptive differences in response to two types of parental alarm calls in altricial nestlings

Chapter 3

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Vertebrate alarm calls can contain information about the type of predator and the degree of danger. The ontogeny of the response to alarm calls has been described as gradual maturation to the response observed in adults. An alternative explanation is that the alarm call response of infants is adapted to the age-dependent risk of each developmental stage. In this study, we tested whether the alarm call response of nestlings of the white-browed scrubwren, *Sericornis frontalis*, is adapted to the predation risk of their developmental stage. As ground predators pose a greater danger to scrubwren nestlings than do aerial predators, we predicted an early development of the reaction to ground alarm calls but not to aerial alarm calls. In a field playback experiment we tested the response of young to aerial and ground alarm calls, each presented in a shorter (less urgent) and longer (more urgent) form. We found that both 5 and 11 day old nestlings responded to ground alarm calls, and did so more strongly to the more urgent playback. By contrast, the response to aerial alarm calls started to develop only towards the end of the nestling stage. Thus, scrubwren nestlings can distinguish between different types of alarm calls and react more strongly to calls warning of a predator posing greater danger, in accord with their age-dependent risk. They furthermore use the length of ground alarm calls as an indicator of the degree of danger.

1. INTRODUCTION

The alarm calls of vertebrates can encode information about the type of predator, the urgency of the response, or both (Macedonia & Evans 1993). Whether alarm calls carry information about urgency or predator class is likely to be adapted to the hunting strategies of each species' predators and the potential for anti-predator responses (Macedonia & Evans 1993; Evans 1997; Fichtel & Kappeler 2002). As the response to alarm calls is potentially costly in terms of time and energy (Curio 1993), and a wrong response might be fatal, the correct identification of type and immediacy of the threat is critical.

The correct response and identification of alarm calls is particularly important for infants and juveniles. Especially in the first weeks of their lives the young of most vertebrates are not able to perform fast and efficient escape manoeuvres, and are often incapable of correctly identifying predators themselves (Seyfarth & Cheney 1980; Mateo 1996a). For example the young of vervet monkeys show limited innate abilities to respond correctly to predators in their environment, and frequently give alarm calls to non-predatory birds (Seyfarth & Cheney 1980; Ramakrishnan & Coss 2000; Hanson & Coss 2001). Many infants thus have to rely on their parents or other group members to identify predators and to assess the degree of danger that they pose. The early development of an appropriate response to adult alarm calls is therefore likely to be under strong selection. Studies on primates and rodents have shown an innate predisposition to respond to species-specific alarm calls (Herzog & Hopf 1984; Mateo 1996b; McCowan *et al.* 2001), but also marked differences between adult and juvenile reactions to alarm calls. The development of an adult-like alarm call response takes 6 to 12 months and may depend on social learning (Hauser 1988; Mateo 1996a; Ramakrishnan & Coss 2000; McCowan *et al.* 2001).

The differences between adult and infant reactions to alarm calls are not necessarily only a sign of an incomplete development, but could be an age-dependent adaptation to differing predation risks and living conditions (Owings & Loughry 1985; Miller & Hicinbothom 1991; Hersek & Owings 1994; Ramakrishnan & Coss 2000; Hanson & Coss 2001). The young of California Ground Squirrels, *Spermophilus beecheyi*, react more strongly to alarm calls given to terrestrial predators than to alarm calls given to aerial predators, opposite to adult behaviour, possibly due to a high infanticide risk (Hanson & Coss 2001). Similar age-dependent changes in the response

to alarm calls are likely to occur in other vertebrate species that experience changing risks during their developmental stages.

The onset of the development of alarm call reactions in birds is potentially adapted to the different developmental histories of precocial and altricial young. The young of precocial and semi-precocial birds respond to alarm calls from the first day post-hatching onwards by freezing and suppressing their vocalizations (Impekoven 1976a; Impekoven 1976b; Miller & Blaich 1986). Contrary to the early development in precocial young, the studies on species with altricial young indicate a later onset of the alarm call response. Ten day old great tit, *Parus major*, nestlings do not react to an adult 'seet' alarm call, of the type used in the context of aerial predators (Ryden 1980), while 16 to 18 day old nestlings suppress their begging vocalizations after playbacks of the same call (Ryden 1978). Khayutin (1985) and Alexandrov (2001) observed that the young of pied flycatchers, *Ficedula hypoleuca*, begin to respond to adult alarm calls, which are given to predators in the air as well as on the ground, with freezing and suppression of vocalization on day 5 to 6. From these studies the question arises whether the timing of the development of the reaction to aerial and ground alarm calls varies depending on the risk posed by the respective predator. For example aerial alarm calls might not be relevant for altricial nestlings, so that the reaction develops later than the reaction towards ground alarm calls. Both alarm calls might be important for precocial young and so the reaction develops pre-hatching. No study on birds has so far tested whether the development of the reaction to alarm calls elicited by different types of predators is adapted to the threat they pose. Such behaviour could be acquired by two different developmental processes that are not mutually exclusive: (1) it could be the result of internal developmental processes that do not rely on environmental stimuli; or (2) based on experience with predator encounters and the subsequent parental response.

The white-browed scrubwren, *Sericornis frontalis*, provides an ideal opportunity to test the adaptiveness of the nestling alarm call response. Scrubwrens lay their eggs in well-concealed nests on the ground so that predators on the ground represent a much more imminent danger for nestlings than flying predators. Predation on scrubwren nests is common and most broods are taken by pied currawongs, *Strepera graculina*, an omnivorous bird that is well known for predation on passerine nests (Wood 1998). Currawongs hunt by sight and sound, and while on the ground react to playbacks of scrubwren nestling calls with search behaviour (Platzen unpubl.). When encountering a predator, adult scrubwrens give two types of alarm calls: ground alarm ('buzz') calls

when a predator moves on the ground or perches in the nest environment and aerial alarm ('trill') calls when a predator flies overhead (Higgins & Peter 2002). The number of elements in an aerial alarm call communicates the response urgency to other adults: a one-element call leads to increased vigilance, while a four-element call prompts immediate flight (Leavesley & Magrath in press). In an earlier study we found that scrubwren nestlings react with almost complete silence to parental ground alarm calls when only 5 days old and show no change in their response up to day 11 (Chapter 2), indicating that the onset of this behaviour happens early in nestling development. Furthermore, the dome shaped nests are usually buried deep inside the leaf litter or inside grass tussocks and nestlings are not exposed to visual stimuli from their environment. Experience of predator encounters is restricted to aural stimuli, so that there is very limited opportunity to learn about predators.

We tested whether the development of the reaction towards ground and aerial alarm calls differs in scrubwren nestlings by playing back both types of alarm calls to 5 and 11 day old nestlings. An adaptive response to an age-dependent risk would be indicated by a stronger response to ground compared to aerial alarm calls throughout the nestling period. We furthermore tested whether an accurate urgency response is present during the nestling stage by playing back long and short alarm calls. Furthermore, to ensure that the nestlings responded to the structural differences of the two call types and not simply to the length of the call playbacks, we matched the length of the short ground alarm and long aerial alarm call playbacks while keeping the amplitude constant. Our predictions were that: (1) ground alarm calls suppress nestling vocalization, and to a greater extent after hearing a more urgent call, and (2) aerial alarm calls do not function as a signal of danger for nestlings regardless of the urgency of the call.

2. MATERIAL AND METHODS

(a) Study species

Adult scrubwrens give two types of alarm calls, 'trills' and 'buzzes' (Higgins & Peter 2002). Trill calls are aerial alarm calls consisting of high frequency, narrow-band elements (duration: 60 - 100 ms; frequency range: 7 – 10 kHz; peak frequency: 7.5 – 7.8 kHz). We will refer to them as aerial alarm calls throughout the manuscript. Buzz calls near the nest are mainly given in the presence of predators on the ground and we will refer to them as ground alarm calls. Ground alarm call elements are generally longer than aerial alarm call elements and have their energy spread over a wide frequency range (duration: 120 - 180 ms; frequency range: 3 – 12 kHz; peak frequency: 6.5 – 8.0 kHz; Platzen unpubl.). Calling can last up to several minutes, depending on how long the danger is present, and can attract other group members (Higgins & Peter 2002). In the absence of adults, nestlings regularly vocalize with short 'peep' calls and call rates can vary from 0 to 200 calls per minute (Platzen unpubl.).

(b) Playback experiment

The experiment was designed to test differences in the reaction of nestlings towards short and long versions of aerial and ground alarm calls. We therefore used four different playback sequences, short and long aerial alarm calls as well as short and long ground alarm calls, for each brood. (1) The short aerial alarm call playback consisted of a three-element trill call that was 337 ± 66 ms (mean ± s.d.) long. (2) The long aerial alarm call playback consisted of eight elements and was 1037 ± 104 ms long. (3) To enable a direct comparison of aerial and ground alarm calls independent of duration and sound output, we designed the short ground alarm call playbacks to be the same duration as the long aerial alarm call playback (mean ± s.d.: 1050 ± 119 ms; 5.5 ± 1.1 elements). The number of elements for long aerial and short ground alarm call playbacks could not be kept constant without changing the natural call rate. (4) The long ground alarm call playback consisted of ten seconds of ground alarm calls. All alarm call playbacks had the same average amplitude. To control for our experimental setup and to make the four playbacks as similar as possible we added a recording of background noise at the beginning of each of the first three alarm call playbacks so that the overall length of all playbacks was ten seconds. We took the background noise from

the original recordings of the alarm calls and edited and amplified it in the same manner as the alarm calls.

We used calls from each brood's own parents to prepare the playback tapes to avoid effects of pseudoreplication (Kroodsma 1998) or parent-offspring recognition (Medvin *et al.* 1992). To gain aerial alarm calls we ran a stuffed currawong that was mounted in a flying position down a fishing line above the nest, while an adult scrubwren was perching close to the nest. All vocalizations of the focal adult were recorded onto a Sony TCD-D100 DAT recorder at 44.1 kHz sampling frequency with two Audio Technica ATM15a condenser lapel microphones attached to the vegetation around the nest. In 13 out of 16 trials the adult reacted by giving aerial alarm calls with 5.8 ± 3.0 elements. We recorded ground alarm calls by placing a mounted currawong close to the nest, similar to the method described in chapter 2. Recordings were digitally transferred onto a Macintosh computer, filtered to remove sound below 2 kHz, and edited for playback using Canary 1.2.4. (Charif *et al.* 1995).

The experiments were conducted between October and December 2002 at 13 different nests when nestlings were 5 and 11 days old. Playbacks were performed following the methods used in chapter 2, but with a Sony CD Walkman D-EJ751 and a Response Dome Tweeter speaker (1.5 – 20 kHz) to playback the alarm calls. The order of playbacks was randomized between, as well as within nests, by using a Latin square design with permutations in a random order. We recorded the vocalizations of each focal brood with an ATM15a microphone placed 16 cm from the nest entrance, connected by a 15 m cable to a DAT recorder. Recordings started one minute before the start of the playback and ended one minute after the end of each playback. Playback amplitudes were kept similar within and between nests: aerial alarm calls 54.7 dB ± 4.2 s.d.; ground alarm calls 54.1 dB ± 3.5 s.d (paired t-test: $t = 1.6$, $p = 0.12$; all amplitudes measured at the nests). These amplitudes lie within the natural range of both calls. The amplitude of background playbacks was 35.8 dB ± 4.8 s.d. following the editing and amplification of alarm calls. Decibel values are re 1 pW/m^2. Recordings were calibrated in Canary using a reference file of known sound pressure level, measured with a Bruel & Kjaer type 2205 sound level meter.

The recordings of the experiments were transferred digitally to Raven 1.0 (Charif & Alberg 2003). We measured all calls given by the nestlings from 15 seconds before the alarm call playback started to 15 seconds after the end of the playback (40

seconds for all playbacks). Spectrograms were created using a filter bandwidth of 124 Hz, frame length 512 points, and the grid resolution set to 86.1 Hz and 5.8 ms. We counted the number of calls before, during and after our playbacks and measured the start time for each call. Call rates during the nine seconds before the start of the playbacks that contained background noise were not statistically different from the call rates during the background noise playback (mean before playback: 1.03 calls per second ± 0.07 s.e.m.; during: 1.04 ± 0.08 s.e.m.; paired t-test: $n = 73$, $t = -0.2$, $p = 0.84$). We therefore concluded that our playback equipment and the background noises of the alarm call sequences had no influence on the nestling response.

(c) Statistical Analysis

We performed experiments at 13 nests but lost one brood around day ten resulting in 25 playbacks with four treatments. We could not analyse one short ground alarm and one long ground alarm both on day 5 because of technical difficulties, and analysed only partly one long aerial alarm on day 11 and one short ground alarm on day 5, following interference by either the parents or environment noise. Due to the unbalanced nature of the data, we used a Linear Mixed Model approach with restricted maximum likelihood estimation (REML) in Genstat 5 (release 4.2, Genstat-Committee 2000). Our models contained 'age' (5 or 11 days), 'type' of playback (aerial, ground), 'duration' of playback (short, long) and all interactions as fixed effects. As random factors we included a nest identifier, to control for variance between nests, and a blocking factor nested within nests that encoded for all treatments at a nest (1-8), to control for variance between treatments at each nest. To assess the significance of the fixed effects we used the sub-model routine in Genstat (Genstat-Committee 2000), and calculated the change in deviance caused by dropping a fixed effect from a full model that contained all significant effects. The resulting change in deviance approximates a χ^2 distribution. In none of our models did the residuals deviate significantly from a normal distribution.

We derived three variables from our initial measurements of the nestling calls as response variates. (1) The call 'change ratio', is the number of calls given during the 15 seconds after each playback divided by the number of calls given during the 15 seconds before each playback (a continuous variable with 0 = complete suppression and 1 = no change). (2) The duration of 'suppression' is the time from the end of the alarm call

playback until resumption of calling. As these two variables were tightly correlated (log correlation: $n = 96$, $r = -0.76$, $p < 0.01$), we also analysed (3) the first factor 'PC1' of a principal component analysis of 'change ratio' and 'suppression' as a combined measure of the intensity of nestling response. Higher values of 'PC1' indicate a stronger response with a greater duration of suppression and fewer calls. The first factor explained 86.5 % of the variance between these two variables with loadings of 0.93 for 'suppression' and -0.93 for 'change ratio'.

3. RESULTS

(a) Discrimination between aerial and ground alarm calls

Nestlings reacted more strongly to ground alarm calls than to aerial alarm calls (response = PC1, effect = type: $\chi^2_1 = 35.49$, $p < 0.001$; figure 1). After hearing the ground alarm playbacks they called less (change ratio, type: $\chi^2_1 = 34.13$, $p < 0.001$; figure 2) and resumed calling after a longer duration of suppression (suppression, type: $\chi^2_1 = 26.36$, $p < 0.001$; figure 3). This response was, over all four playbacks, independent of the age of the nestlings (PC1, type*age: $\chi^2_1 = 2.2$, $p = 0.14$; change ratio, type*age: $\chi^2_1 < 0.01$, $p = 0.96$; latency, type*age: $\chi^2_1 = 2.03$, $p = 0.15$).

Restricting the analysis to only long aerial and short ground alarm calls, the two playbacks of similar duration, showed a difference in response according to nestling age. Five day old nestlings did not react to long aerial alarm calls but responded to short ground alarm calls. By contrast, 11 day old nestlings showed only a small difference in the response to the two playbacks. They increased their reaction to long aerial alarm calls and reduced the reaction to short ground alarm calls compared to the 5 day old nestlings (PC1, type*age: $\chi^2_1 = 4.63$, $p = 0.03$; figure 1). The duration of suppression increased in 11 day old nestlings in response to long aerial alarm calls and decreased less strongly after short ground alarm calls compared to 5 day old nestlings (suppression, type*age: $\chi^2_1 = 7.15$, $p < 0.01$; figure 3). There was no detectable effect on the number of calls (change ratio, type*age: $\chi^2_1 = 1.05$, $p = 0.31$; figure 2). Overall, these age differences show that on day 11 nestlings had started to react to aerial alarm calls.

(b) Effect of call length on nestling reaction

Nestlings responded more intensely to playbacks of long alarm calls than playbacks of short alarm calls (PC1, duration: $\chi^2_1 = 10.91$, $p < 0.001$; figure 1). They reduced their calling activity significantly more after hearing long alarm calls (change ratio, duration: $\chi^2_1 = 4.62$, $p = 0.03$; figure 2) and increased the time during which calling was suppressed (suppression, duration: $\chi^2_1 = 14.66$, $p < 0.001$; figure 3). This distinct response to short and long calls was significantly stronger in old nestlings than in young nestlings (PC1, duration *age: $\chi^2_1 = 6.63$, $p = 0.01$; figure 1) and old nestlings responded with longer suppression times compared to young nestlings after hearing

long alarm calls (suppression, duration *age: $\chi^2_1 = 14.66$, $p < 0.001$; figure 3). The different reaction of young and old nestlings appeared only as a non-significant trend in the data for the number of calls (change ratio, duration *age: $\chi^2_1 = 2.53$, $p = 0.11$; figure 2). The change in sensitivity towards longer alarm calls in 11 day old nestlings appeared to be mainly influenced by an intensified reaction towards long aerial alarm calls that did not appear in 5 day old nestlings. The reaction towards ground alarm calls of different duration was similar in young and old nestlings, but with a more pronounced distinction between short and long calls in old nestlings.

4. DISCUSSION

Scrubwren nestlings showed a much more intense response to ground than to aerial alarm calls throughout the nestling period. Playbacks of ground alarm calls suppressed the vocalization of 5 and 11 day old nestlings whereas there was no response to aerial alarm call playbacks in 5 day old nestlings and only partial suppression of calls in 11 day old nestlings. In contrast to nestlings, adults respond to multi-element aerial alarm calls with immediate flight (Leavesley & Magrath in press). As predators moving on the ground pose a far greater threat to the nestlings than aerial predators, but the reverse is likely to be true for adults, our data indicate that the alarm call response in scrubwren nestlings is adapted to their developmental stage, rather than being an imperfect version of the adult reaction to alarm calls. The nestlings furthermore developed an urgency response towards ground alarm calls by suppressing their vocalization for longer and calling less after hearing long alarm calls compared to short alarm calls. These findings show that the ability to respond to alarm calls carrying information about the type of threat and the urgency of the response can develop early in life.

The differentiation between parental alarm calls signalling different types of threat might be a common adaptation during the development of young birds. Similar to our first study (Chapter 2), nestlings showed a consistent strong response to the 10 second ground alarm playback that was fully developed in 5 day old nestlings. In a natural situation ground alarm calls are given as long as a predator is present in the nest environment, up to several minutes (Platzen unpubl.). The suppression of nestling vocalization in the presence of a searching predator is thus likely to be very efficient. A response to the aerial alarm playbacks was only apparent in 11 day old nestlings, even then only when the playback was representative of a very urgent alarm signal. The threat that flying predators pose to scrubwren nestlings does not change over the course of the nestling stage, so that the observed response to aerial alarm calls in older nestlings probably foreshadows the change in risk after fledging. We predict that the response to aerial alarm calls increases over the last days before fledging and that fledglings respond more strongly to aerial alarm calls than to ground alarm calls, as the threat from flying predators is stronger for fledglings than for nestlings. This prediction is consistent with the findings of the limited number of studies on other bird species. Pied flycatchers start to respond to parental alarm calls that are given to predators that

are a threat to the nest on day 4 of nestling age, well before fledging (Khayutin 1985; Alexandrov *et al.* 2001). Playback experiments with great tits have shown a lack of response to aerial alarm calls for young nestlings but a well developed response before fledging (Ryden 1978; Ryden 1980). Further experimental work on altricial species with differing nesting ecology and warning call systems is needed to test this hypothesis.

The differential response to aerial and ground alarm calls in scrubwren nestlings was not caused by an inability to hear high frequencies. In pied flycatcher nestlings, for example, measurements of brain potentials have shown that the ability to hear high frequencies increases with age and that 4 to 7 day old nestlings are highly sensitive only to frequencies between 1 and 5 kHz (Khayutin 1985). Nevertheless, a species' hearing sensitivity is often correlated with the highest frequencies used in the vocal repertoire (Dooling 1982), and in chickens and mallard ducks the hearing ranges of young match the frequencies of parental food and contact calls (Saunders *et al.* 1974). A commonly used call during parental feeding visits in scrubwrens is the 'chip' call that has its main energy in a frequency range similar to the aerial alarm calls (7 – 9 kHz; Higgins & Peter 2002). During 38 trials from 2001 to 2003 we played back chips with a mean peak frequency of 8.2 kHz ± 1.0 s.d. to scrubwren nestlings on day 5 and found that peep call rates were higher during the chip playbacks than during the 15 seconds beforehand, indicating that the nestlings responded to the playbacks (mean before: 0.52 calls per second ± 0.09 s.e.m, after: 1.04 ± 0.18 s.e.m.; paired t-test: $t = -3.4$, $p = 0.002$). It seems unlikely that another parental call in the same frequency range cannot be heard. Thus, behavioural distinction rather than developmental constraints appear to have led to the different responses to aerial and ground alarm calls in scrubwren nestlings.

Nestlings responded to alarm calls of different duration with different levels of vocal inhibition. This response was independent of the context of the calls because other parental behaviour or cues from a predator were not present. The greater response to longer calls seems adaptive if longer calls signal a predator remaining near the nest for longer. We have not yet tested whether ground alarm calls encode information about the distance of a predator.

The idea that the response to alarm calls in infants and juveniles is the subject of developmental adaptation has been formulated for mammals (Owings & Loughry 1985; Miller & Hicinbothom 1991; Hersek & Owings 1994; Hanson & Coss 2001) and

precocial birds (Miller & Hicinbothom 1991) and seems likely to be widely applicable. The difference in the reaction to aerial and ground alarm calls in scrubwren nestlings and adults shows intriguing similarities to the alarm call response and production of juvenile and adult California ground squirrels (Hanson & Coss 1997; Hanson & Coss 2001). These parallels indicate that predation pressure leads not only to similar signalling systems across a wide range of vertebrates (Macedonia & Evans 1993; Evans 1997) but also to similar developmental histories. The mechanisms are nevertheless likely to differ. For most mammal species it has been suggested that social learning is necessary to develop a functional alarm call response. In scrubwrens it is more likely that the maturation of the alarm call response is driven by internal developmental processes rather than learning, as visual cues from the environment are virtually absent during the nestling stage and the response to ground alarm calls is fully developed when nestlings are only 5 days old. Nestlings cannot see any predators or observe the behaviour of their parents during a predator encounter due to the enclosed nature of the dome shaped nest and the hidden nest location. Studies on precocial bird species have shown tat learning is not necessary for the development of an alarm call response (Impekoven 1976b; Miller & Blaich 1986). A comparative approach to developmental processes in avian and mammalian alarm call systems seems promising to further our understanding of the evolutionary processes shaping alarm call behaviour.

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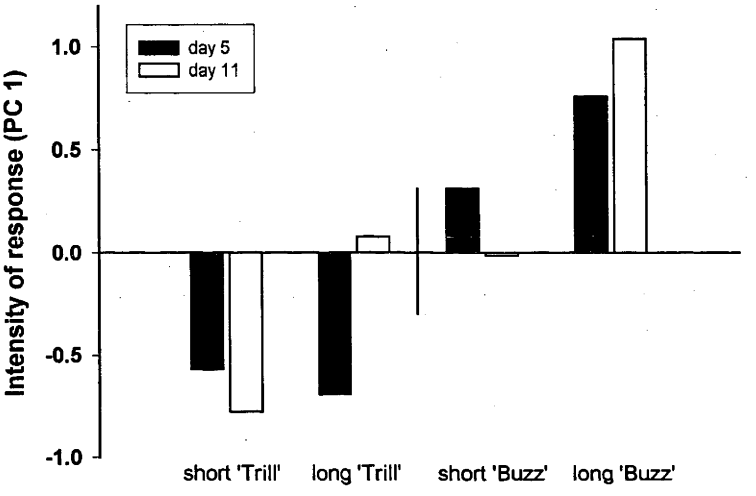

Figure 1: Response of 5 (solid bars) and 11 (open bars) day old nestlings to playback of alarm calls. Intensity of the response shown as the first factor of a principle component analysis of 'number of calls' and 'latency'; more positive values indicate a greater suppression of vocalization. Bars show estimated means of the REML analyses; lines between bars show the least significant difference (two times the standard error of the difference).

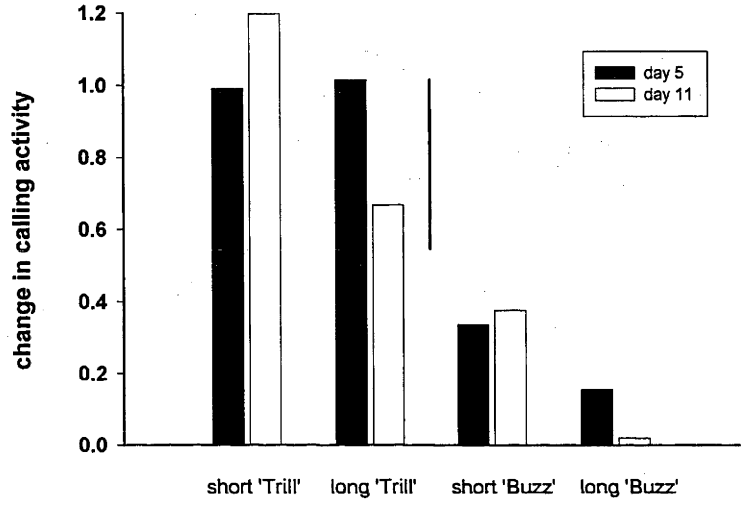

Figure 2: Response of 5 (solid bars) and 11 (open bars) day old nestlings to playback of alarm calls. Change in vocal activity shown as the ratio of the number of calls given during the 15 second interval after the experimental playbacks divided by the number of calls given in the 15 second interval before the playbacks. A value of 0 indicates complete suppression of vocalization and a value of 1 indicates no change at all. Bars show estimated means of the REML analyses; lines between bars show the least significant difference (two times the standard error of the difference).

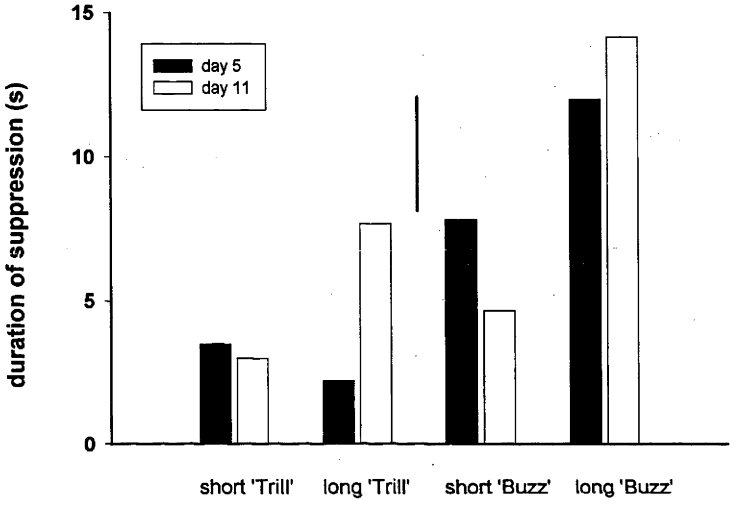

Figure 3: Response of 5 (solid bars) and 11 (open bars) day old nestlings to playback of alarm calls. Duration of suppression after the end of an alarm call playback; greater values indicate greater suppression of vocalization.

Dynamic structural changes of avian vocal signals in response to the threat of predation

Chapter 4

Many acoustic signals have evolved to minimize costs of overhearing from predators and parasites. Dynamic changes in call structure can potentially act as a behavioural response to manage costs and benefits of continued signalling in the presence of a predator or parasite. Nestlings of the white-browed scrubwren, *Sericornis frontalis*, inhibit their calling activity adaptively in response to parental alarm calls signalling different levels of threat. They suppress non-begging calls that are used in the absence of parents but do not change the begging calls that are given during feeding visits. In this study we tested whether nestlings use dynamic changes in call structure as an additional behavioural response to parental alarm calls. We found that nestlings responded to aerial and ground alarm calls with an increase in frequency and a change in length of their non-begging calls that may lead to a reduction in detectability and localizability. We suggest that dynamic changes in call structure and the inhibition of calling activity together optimize the trade-off between the benefits of continuous signalling and the costs of predation. In contrast to non-begging calls, nestlings did not change the structure of their begging vocalizations, supporting earlier findings that the presence of an adult acts as an 'all clear' signal.

1. INTRODUCTION

Acoustic communication has the inherent danger that individuals other than the intended receiver overhear the signals and take advantage of the information (Bradbury & Vehrencamp 1998; Zuk & Kolluru 1998). The structure of many animal signals is thus the result of a trade-off between predator or parasite avoidance and the need to transfer information efficiently to the receiver (Lima & Dill 1990). The alarm calls that are used by many bird species to warn of aerial predators, for example, have a structure that is designed to be difficult for predators to hear while signalling danger efficiently to conspecifics (Marler 1957; Klump & Shalter 1984; Wood *et al.* 2000). Behavioural adaptations that impede the detection and localization of acoustic signals by predators or parasites can take place on an evolutionary timescale, shaping the signalling repertoire of a species (Bradbury & Vehrencamp 1998), or on an ecological timescale, leading to dynamic changes in calling activity or signal design according to current risk (Lima & Dill 1990).

Short-term behavioural adaptations to predator or parasite presence can be inhibition of calling activity or dynamic changes in the signal structure. The exploitation of vocal signals by predators and parasites has mainly been studied in the context of sexual signals (reviewed in Zuk & Kolluru 1998). The most common behavioural adaptation employed as a short-term response to predation or parasitism threat is an inhibition of calling (Zuk & Kolluru 1998). If the caller selectively inhibits call elements that are more conspicuous than others, vocal inhibition can lead not only to a quantitative but qualitative change of signal output. For example, the male Tungara frog, *Physalaemus pustulosus*, uses low frequency elements in its advertisement call to attract females. Hunting bats can easily locate the low frequencies and male frogs inhibit the revealing elements when they detect a predator (Ryan *et al.* 1982). Dynamic structural changes of call elements have recently been reported in alarm calls, another well-studied group of acoustic signals that are under strong selective pressure to avoid detection by a predator (Marler 1957; Klump & Shalter 1984; Wood *et al.* 2000). Bayly and Evans (2003) showed that male domestic chickens, *Gallus gallus*, changed the structure of alarm call elements during a bout by reducing the introductory pulse, and interpreted this behaviour as an adaptation to an increased risk of detection after the initial call had been given. In the white-browed scrubwren, *Sericornis frontalis*, Leavesley and Magrath (in press) found that the minimum frequency of aerial alarm

calls increased with increasing urgency and predator proximity, an adaptation that potentially reduces the risk of overhearing by a predator. Similar observations have been recorded for Mexican chickadees, *Parus sclateri* (Ficken 1990). Due to their mode of sound production passerine birds offer an excellent opportunity to test for vocal plasticity. The syringeal structures that passerines use to produce vocal signals allow for a precise control of time and frequency characteristics that can influence detectability and localizability of their calls (Gaunt & Nowicki 1998).

Detection of a sound depends on the characteristics of the signal as well as the sensory properties of the receiver (Klump & Shalter 1984). Sound detection is mainly determined by amplitude and frequency of the signal as well as the background noise level. Low frequency sounds attenuate less than sounds of higher frequency, making them easier to detect at a distance (Klump & Shalter 1984). Furthermore, the critical ratio of signal to background noise amplitude increases in most bird species by 2-3 dB per octave (Dooling *et al.* 2000), which makes high frequency sounds generally harder to detect for avian predators especially at a distance (for exceptions see: Klump & Shalter 1984; Dooling *et al.* 2000). The audibility curves (minimum audible sound pressure) for most studied bird species increase sharply above 5 kHz showing that hearing capacities are best in the lower to middle frequencies and least developed for high frequencies (Dooling *et al.* 2000). To reduce the detectability of an acoustic signal, the structure should be changed into the direction of low amplitude, high frequency sounds.

To localize a sound source a receiver has to determine the angle between its own position and the sound source (azimuth) as well as the elevation and distance of the sound source (Nelson & Stoddard 1998). All three measures are influenced by amplitude, frequency and length of the signal (Klump 2000). Azimuth resolution depends also on the head size of the receiver and consequently abilities for sound localization vary greatly between species. Eastern towhees, *Pipilo erythrophtalmus,* for example, can determine the angle of a sound source that produces a conspecific call with an accuracy of ± 5° even when the speaker was turned off after the bird had left the perch (Nelson & Stoddard 1998). The distance resolution was of similar accuracy with an average of 7% of the total speaker distance (Nelson & Stoddard 1998). If a sound source produces sound continuously accurate azimuth or distance resolution might not even be required because the bird can simply home in on the signal. Most bird species

that have been tested under natural conditions show the ability to home in on a continuous sound source (Klump 2000).

The vocalizations of nestling birds are acoustic signals that for a long time have been suspected to attract predators (Haskell 2002). More intense and vigorous begging is related to nestling hunger and leads to an increase of parental provisioning (Budden & Wright 2001). Playback experiments with artificial nests and nest sites have shown that nestling begging calls can potentially attract predators to the nest (Haskell 1994; Leech & Leonard 1997). The results of across species comparisons as well as playback experiments have furthermore suggested that nestlings of species with a high predation risk have begging calls that are less conspicuous and show signs of an evolutionary adaptation (Briskie *et al.* 1999; Haskell 1999). Not much attention has been paid to nestling vocalization besides begging. Two recent studies suggest that non-begging vocalization is mainly erroneous begging and only relevant to predation if the nestlings attract predators to the nest by responding to wrong stimuli (Leonard & Horn 2001; Wright *et al.* 2002).

Scrubwren nestlings vocalize in the absence of parents with calls different from begging calls (Maurer *et al.* 2003) and suppress non-begging but not begging vocalization in response to parental ground alarm calls (chapter 2). These results indicate that non-begging rather than begging calls have the potential to lead predators to scrubwren nests. Nevertheless, many broods do not change their calling activity (number of calls per unit time), or simply reduce the number of calls after hearing aerial alarm calls and short playbacks of ground alarm calls (chapter 3).

The aim of the current study was to examine whether scrubwren nestlings use dynamic changes in their call structure to reduce conspicuousness if they continue signalling after hearing alarm calls. We tested specifically whether nestlings change (1) the call length, (2) the frequencies or (3) the amplitude of their non-begging as well as begging vocalization in response to parental alarm calls. We played back short (low intensity) and long (high intensity) aerial and ground alarm call playbacks and recorded the immediate effect on the non-begging vocalization. The effect on begging calls was determined during and after a subsequent playback of parental contact and provisioning calls that imitated the arrival of a feeding parent. Our predictions were that nestlings would respond to the level of threat by changing the structure of non-begging calls by increasing the frequencies as well as reducing the length and the amplitude. These

changes should be more pronounced after ground alarm calls than after aerial alarm calls. We expected no changes in the structure of begging calls.

2. METHODS

(a) Study species

The white-browed scrubwren is a cooperative breeding passerine with an average clutch size of three eggs (Magrath *et al.* 2000; Magrath 2001). The dome shaped nest is usually well hidden in the leaf litter or in grass tussocks on or near the ground. Nest predation rates are five times higher during nestling stage than during incubation (Magrath unpubl.). The majority of predation events in our study site, the Australian National Botanic Gardens (35°16'S, 149°06'N), were caused by the pied currawong, *Strepera graculina*, a common avian predator of passerine nests (Wood 1998). When encountering a predator close to the nest adults give two different types of alarm call (Higgins & Peter 2002). The high frequency 'trill' call consists of three to twelve short elements and is evoked by the sight of a flying predator (Leavesley & Magrath in press). We will refer to it as the 'aerial alarm call' throughout this manuscript. A predator moving or perching on the ground evokes the 'buzz' call that consists of short broadband elements. Calling can last up to several minutes depending on how long the predator is present. We will refer to it as the 'ground alarm' call. When adults approach a nest with food they usually start to give contact calls ('chips') several meters away from the nest and nestlings often react with an increased rate of vocalization. After landing at the nest entrance adults give provisioning calls that induce begging from nestlings (Higgins & Peter 2002).

Scrubwren nestlings use two types of vocalizations, non-begging calls in the absence of parents and begging calls during feeding visits (Higgins & Peter 2002). For both call types the calling activity of nestlings depends on the hunger level (Maurer *et al.* 2003). Non-begging signals are repeated with rates of up to 3 calls per second and per brood for long periods of time in the absence of parents (Maurer *et al.* 2003; Platzen unpubl.). These 'peep' calls have their main energy around 6.98 kHz ± 0.64 s.d. (this study: n = 1545; figure 1a) and are short (mean: 77 ms ± 29 s.d.) and high pitched (min.: 6.01 kHz ± 0.73 s.d.; max.: 7.86 kHz ± 0.989 s.d.; range: 1.81 kHz ± 0.89 s.d.). Although the signal structure indicates a low detectability, the high repetition of signals and the long duration of calling bouts may facilitate detection as well as localization. A repeated signal can be detected more easily than its structure suggests because background noise levels usually fluctuate over time, making the signal more likely to

stand out (Klump & Shalter 1984). Not surprisingly, scrubwren nestlings suppress their non-begging vocalization when they hear playbacks of parental ground alarm calls, especially when the alarm calls are long and potentially indicate that a predator remains close to the nest (chapter 2, 3).

Scrubwren begging signals consist of long, high amplitude, broad frequency calls that, if given within the hearing range of a predator, would very likely betray the nest location (Maurer *et al.* 2003). These 'whine' calls have their main energy around 7.54 kHz ± 0.84 s.d. (this study: n = 778; figure 1b), are longer than peeps (302 ms ± 154 s.d.), of wider range (min.: 6.15 kHz ± 0.91 s.d.; max.: 8.71 kHz ± 0.88 s.d.; range: 2.56 ± 1.18 s.d.), and usually trail off into peeps (Higgins & Peter 2002). Despite their conspicuousness, there is minimal reduction in begging activity after hearing parental ground alarm calls, indicating that parental visits to the nest act as an 'all clear' signal (chapter 2).

(b) Playback experiment

To test whether the nestlings change the structure of their non-begging and begging calls according to the type and length of parental alarm calls, we used four different alarm call playbacks that were all followed by a sequence of contact and provisioning calls. The four different playback sequences consisted of short and long aerial alarm calls as well as short and long ground alarm calls for each tested brood. (1) The short aerial alarm playback was made up of a three element trill call that was 337 ± 66 milliseconds long. This length was chosen to minimise the chance that the nestlings did not hear our playbacks. (2) The long aerial alarm playback consisted of eight elements and was 1037 ± 104 milliseconds long. This is a comparatively strong stimulus that, nevertheless, is within the natural range of adult aerial alarm calls when warning near the nest or fledglings (up to 12 elements, Platzen unpubl.). (3) We adjusted the short ground alarm playback to the same length as the long aerial alarm playback independent of the number of elements, 1050 ± 119 milliseconds and 5.5 ± 1.1 elements. (4) The long ground alarm playback consisted of 10 seconds of alarm calls. All alarm call playbacks had the same average amplitude. To control for our experimental set up and to make the four playbacks as similar as possible we added a recording of background noise at the beginning of each of the first three alarm call playbacks so that the overall length of all playbacks was 10 seconds. We took the

background noise from the original recordings of the alarm calls and edited and amplified it in the same manner as the alarm calls.

Each 10 second alarm call playback was followed by a 15 second break without any playback and a 3.5 second sequence of parental contact and provisioning calls. The period of silence was used to record the non-begging nestling vocalizations immediately after the alarm calls, and it was designed to be short enough to ensure that any effect of the preceding playbacks was still present at the beginning of the following contact and provisioning call playback. The parental feeding vocalizations consisted of four chip calls followed by a provisioning call, which is a common pattern of adult vocalizations given on arrival at the nest with food. The begging response of the nestlings was recorded for 15 seconds following the first chip call.

We used calls from each brood's own parents to prepare the playback tapes, thereby avoiding effects of pseudoreplication (Kroodsma 1998) or parent-offspring recognition (Medvin *et al.* 1992). All parental vocalizations were recorded onto a Sony TCD-D100 DAT recorder at 44.1 kHz sampling frequency with Audio Technica ATM15a condenser lapel microphones. We recorded the alarm calls when nestlings were 3 or 4 days old. To gain aerial alarm calls we ran the taxidermic mount of a currawong that was fixed in a flying position down a fishing line above the nest, while an adult was perching close by. We recorded ground alarm calls by placing a currawong mounted in a sitting position close to the nest on the ground while the parents were foraging and then waited until the parents returned and gave ground alarm calls. The adults' chip and provisioning calls were recorded during natural feeding visits, with the microphone 16 cm from the nest entrance. Recordings were digitally transferred onto a Macintosh computer, filtered to remove sound below 2 kHz, and edited for playback using Canary 1.2.4. (Charif *et al.* 1995).

The experiments were conducted between October and December 2002 at 13 different nests when nestlings were 5 and 11 days old. We performed playbacks with a Sony CD Walkman D-EJ751 and a Response Dome Tweeter speaker and recorded the nestling vocalizations with an ATM15a microphone 16 cm from the nest entrance, connected by a 15 m cable to a DAT recorder. After the set up, we waited 30 to 45 minutes and then started each playback sequence only when the adults were out of our hearing range (at least 20 meters). We did this to avoid the possibility that the behaviour of the nestlings was influenced by any parental calls or activities, or that the adults overheard our alarm call playbacks. The order of playbacks was randomised between, as

well as within nests, with help of a Latin square design with permutations in a random order. Recordings started one minute before the start of the playback and ended one minute after the end of each playback. Calls were played back to the nestlings with similar levels for all alarm call playbacks within one experiment: aerial alarm calls 54.7 ± 4.1 dB and ground alarm calls 53.5 ± 2.8 dB, measured at the nest. These amplitudes matched the natural sound levels of aerial alarm calls (mean 60 ± 6 dB 3 - 5 m away from the source; Leavesly & Magrath in press) and ground alarm calls (54 ± 4 dB 4 - 7 m away from the source; chapter 2). The amplitude of background playbacks was 35.8 ± 4.8 dB following the editing and amplification of alarm calls. Decibel values are re $1pW/m^2$. Recordings were calibrated in Canary using a reference file of known sound pressure level, measured with a Bruel & Kjaer type 2205 sound level meter. Our technical equipment and the background noises of the alarm call sequences had no influence on the nestling response (see chapter 2 for details).

Recordings of the experiments were transferred digitally to Raven 1.0 (Charif & Alberg 2003). We measured all calls given by the nestlings from 15 seconds before the alarm call playback started to 15 seconds after the end of the playback (60 seconds for all playbacks). Spectrograms were created using a filter bandwidth of 124 Hz, frame length 512 points, and the grid resolution set to 86.1 Hz and 5.8 ms. We measured the start time, length, minimum, maximum and peak frequency as well as average and peak amplitude for each call to test for changes in call structure in response to our playbacks. We measured overlapping vocalizations when more than one nestling called at a time, but excluded these calls from the amplitude and peak frequency analysis.

(c) Statistical analysis

We performed experiments at 13 nests but lost one brood around day 10 resulting in 25 playbacks with four treatments. One short ground alarm and one long ground alarm treatment, both on day 5 but at different nests, could not be analysed because of technical difficulties. One long aerial alarm treatment on day 11 as well as one short ground alarm treatment on day 5 could not be analysed following interference by either the parents or environment noise. We analysed the effects of our playbacks on the length, frequencies and amplitude of non-begging and begging vocalizations separately.

(i) *Non-begging vocalization*: In response to 31 of 98 treatments the reaction of nestlings was silence (short aerial alarm = 2, long aerial alarm = 6, short ground alarm = 5, long ground alarm = 18) so we omitted these trials from the analysis, resulting in a small sample size for the long ground alarm playbacks (day 5 = 4 nests, day 11 = 2 nests). Due to the unbalanced nature of the data, we used a Linear Mixed Model (LMM) approach with Restricted Maximum Likelihood Estimation (REML) in Genstat 5 (release 4.2, Genstat-Committee 2000). We tested for changes in the length, frequencies and amplitude of non-begging calls. Our models contained 'age' (5 or 11 days), 'type' of alarm playback (aerial vs. ground), 'duration' of alarm playback (short vs. long), 'timing' of nestling calls (before vs. after the alarm playback) and all interactions as fixed effects. A nest identifier and a blocking factor, encoding for the four treatments on two days and the two possible response times (8 times before and 8 times after = 16 levels), nested within the nest identifier were included as random factors to control for the variance between nests as well as between treatment levels within nests. Variance components of the random effects were estimated using the REML procedure in Genstat and showed an influence on all our models for both factors. To assess the significance of the fixed effects we used the sub-model routine implemented in Genstat (Genstat-Committee 2000), and calculated the change in deviance caused by dropping a fixed effect from a full model that contained all significant effects. In none of the models did the residuals deviate significantly from a normal distribution.

(ii) *Begging vocalization*: To test the influence of the alarm call playbacks on the begging activity of the nestlings, we calculated for each playback the response 'latency' as the time from the start of the contact and provisioning call playback to the beginning of the first nestling call. A second measure of nestling response was the 'cumulative length' of all begging calls given in response to the contact and provisioning calls. For the analysis we used a LMM with age, type and duration of alarm calls as well as fixed effects and all interactions. A nest identifier and a blocking factor encoding for all treatments within one nest (1 – 8), nested within nest identifier, were included as random factors. We tested for changes in the length, frequencies and amplitude of begging calls in a further analysis using the same model structure. In none of the models did the residuals deviate significantly from a normal distribution.

3. RESULTS

a) Effects of alarm calls on non-begging calls

Call length: The length of the nestlings' calls depended on the type of alarm call that was played back and nestling age. After hearing aerial alarm calls the length of nestling calls increased and after hearing ground alarm calls the length of nestling calls decreased compared to the length of calls before the playbacks (timing*type: $\chi_1^2 = 7.8$, $p < 0.01$; figure 2). Call length also decreased strongly with age ($\chi_1^2 = 48.4$, $p < 0.001$; figure 2).

Main frequencies: Nestlings of both ages raised the minimum and peak frequencies of their calls significantly after hearing alarm calls, indiscriminate of type or length of the playback. The mean minimum frequency increased by 142 Hz ± 67 s.e.d. ($\chi_1^2 = 4.4$, $p = 0.04$) and the mean peak frequency increased by 191 Hz ± 84 s.e.d.; ($\chi_1^2 = 5.1$, $p = 0.02$; figure 3). The increase in mean maximum frequency, 207 Hz ± 108 s.e.d., was bordering on significance ($\chi_1^2 = 3.7$, $p = 0.06$). The general increase of call frequencies left the frequency range of calls unaffected by the playbacks, while it decreased as nestlings got older ($\chi_1^2 = 7.0$, $p < 0.01$). The main frequencies of the calls shifted down with age (minimum: $\chi_1^2 = 7.4$, $p < 0.01$; maximum: $\chi_1^2 = 13.35$, $p < 0.001$; peak: $\chi_1^2 = 12.9$, $p < 0.001$; figure 3).

Amplitude: The average and peak amplitude of calls were unaffected by the playbacks but increased with nestling age (average: $\chi_1^2 = 9.4$, $p < 0.01$; peak: $\chi_1^2 = 10.4$, $p = 0.001$).

b) Begging vocalization

Response latency and begging activity: The time that it took the nestlings to respond after hearing the first contact call from the playbacks was longer after the ground alarm than after the aerial alarm playbacks ($\chi_1^2 = 7.3$, $p < 0.01$; figure 4a) and increased with the duration of the alarm calls ($\chi_1^2 = 6.4$, $p = 0.01$; figure 4a). Response latency was not influenced by the age of the nestlings. Unlike response latency the cumulative length of all given calls, a measure of begging intensity, decreased strongly as nestlings got older ($\chi_1^2 = 42.45$, $p < 0.001$; figure 4b), and was unaffected by the alarm call playbacks.

Call structure: The length of the calls, all main frequencies and frequency range remained unaffected by the alarm call playbacks but were strongly affected by nestling age. Call length decreased with age ($\chi_1^2 = 53.62$, $p < 0.01$, estimated change = -129 ms ± 31 s.e.d.) and so did all frequency measures (minimum: $\chi_1^2 = 5.7$, $p = 0.02$; maximum: $\chi_1^2 = 13.77$, $p < 0.001$; peak: $\chi_1^2 = 18.21$, $p < 0.001$; range: $\chi_1^2 = 13.16$, $p < 0.001$). The amplitude of the begging calls did not change in response to the alarm call playbacks or with nestling age.

4. DISCUSSION

Scrubwren nestlings responded to parental alarm call playbacks by changing the length and frequencies of their non-begging calls in a way that potentially leads to a decrease in detectability and localizability of the signals. Thus, dynamic structural changes of vocal signals can be an additional form of behavioural adaptation that scrubwren nestlings utilize to reduce the conspicuousness of their vocal signals. We suggest that in combination with the previously shown inhibition of signalling activity (chapter 2, 3), dynamic structural changes increase the nestlings' potential to optimize the trade-off between predation costs and benefits of their vocal signals.

Scrubwren nestlings responded to parental alarm calls with a change in call frequencies. Nestlings raised the principal frequencies of their remaining non-begging calls in response to all alarm call playbacks independent of alarm call type or duration. Interestingly, the frequencies were raised even if the calling activity remained unchanged (day 5 aerial alarm playbacks) or was slightly increased (day 11 short aerial alarm playback). This indicates that an increase in frequencies is a general response to disturbance at the nest that is employed even if the situation is not assessed as an immediate threat. An increase in signal frequency leads to a stronger attenuation of the signal in the environment and consequently to a decrease in detectability and localizability (Klump & Shalter 1984; Klump 2000).

To what extent the observed average rise in peak frequency of 190 kHz impedes the ability of an acoustically hunting predator to home in on the signal depends on the sensory properties of the predator and the distance of the predator to the nest. The hearing range and signal to noise ratio of the principal predator on scrubwren nests, the pied currawong, is not known. Nevertheless, first trials with outdoor playbacks of nestling vocalization have shown that currawongs can detect and home in on non-begging as well as begging vocalizations that are played back with a natural sound level (Platzen unpubl.).

The distance of the predator to the nest is likely to determine the intensity of the parental alarm calls. Experiments with adult scrubwrens have shown that the length of aerial alarm calls encodes for the degree of danger (Leavesley & Magrath in press). The nestlings' response to urgent ground alarm calls that are likely to indicate the close proximity of a predator to the nest and/or its continued presence is almost invariably complete silence (chapter 2). Nestling vocalization is most likely to prevail when a

predator is further away from the nest. At an increased distance, even a slight change in signal frequency has the potential to reduce conspicuousness (Klump & Shalter 1984). The observed change in call structure could thus be an adaptive response. We suggest that the nestling response to parental alarm calls is a multi-stage process that combines dynamic changes in call structure and the reduction of calling activity to optimize the trade-off between the benefits of continuous signalling and the costs of predation.

The opposite changes in call length in response to aerial and ground alarm call playbacks suggests that call length is adjusted not as a general response to disturbance but depending on the level of threat. Predators on the ground pose a much greater danger to nestlings than flying predators, which are unlikely to hear nestling calls. The question remains why nestlings, upon hearing aerial alarm calls, adjust some structural parameters (frequencies) in a way that makes the calls less conspicuous and another parameter (length) in a way that makes the calls more conspicuous. One possible explanation is that a shift to higher frequencies leaves signalling efficiency unaffected at a close range but has a strong effect on detectability in a distance and is thus used regardless. A reduction in call length potentially affects signalling efficiency on a close range as well as making the signal more cryptic in a distance. In urgent situations, a decrease of call length could add another level of crypsis, before call rate is reduced to a minimum. In the absence of any information about the function and benefits of the non-begging vocalization we can only speculate about the effects of changes in the call structure on this particular signalling process. Another explanation for the observed results could be that the neuronal control over the different spectrotemporal call features is more or less variable. The young of several bird species have been shown to react to alarm calls with a decrease in heart rate and a related locomotor inhibition (Khayutin 1985; Evans & Gaioni 1990). If an increase in call frequency is an invariable response to alarm calls, connected to a general state of alertness, but call length is still variable, nestlings could use an increase in call length during less urgent situations to counteract the potential negative effect of increased frequencies on signalling efficiency. The observed lack of variation in call amplitude could likewise be a consequence of either costs due to loss in signalling efficiency or decreased neuronal control due to a freezing response.

The results of our study highlight the potential importance of dynamic changes in call structure as an adaptive response to predation threat during signalling. Not many studies have found evidence for short-term responses to predator threat other than signal

inhibition. The males of the Tungara frog, although essentially inhibiting calling activity, change the frequencies of their signals by avoiding low frequency elements ('chucks') of their calls (Ryan *et al.* 1982). Females prefer males that give 'chuck' calls because these calls carry information about the size of the male. Bats can locate males that give 'chucks' easier than other males (Ryan *et al.* 1983) and frogs can negotiate the trade-off between efficient signalling and predation with this short-term behavioural adaptation. Male fowl use a similar strategy but actually change the structure of their aerial alarm calls during a calling bout, presumably because they are at a higher risk of being attacked after they have given the first call (Bayly & Evans 2003). By suppressing the high amplitude, broad-band pulse from all but the first call element of a bout, the males may be able to continue signalling without endangering themselves. Many aerial predators have difficulties localizing high frequency calls (Jones & Hill 2001), and structural changes in alarm call design have been observed in scrubwrens and chickadees (Ficken 1990; Leavesley & Magrath in press).

Our study provides further evidence that birds can use dynamic structural changes of vocal signals to resolve the trade-off between signalling activity and predation risk. Our results are unique because they indicate that scrubwren nestlings use a combination of inhibition and dynamic structural changes of vocal signals. Furthermore, the affected calls are neither sexual nor alarm calls (for an example of predation related to the structure of contact calls see Krams 2001). We found that the response to alarm calls was largely unaffected by age and already well developed when the nestlings had just opened their eyes (day 5). Even with their eyes open nestlings can not see any predators or observe the behaviour of their parents during a predator encounter due to the enclosed nature of the dome-shaped nest and the hidden nest location. It is therefore likely that the development of this anti-predator response is largely based on internal developmental mechanisms. Further research is required to assess whether learning processes are at all necessary for the maturation of this behaviour complex.

Nestlings did not respond to parental alarm calls with a change in their begging signals although they were still under the influence of the alarm calls when the contact and provisioning calls started. The lack of variation in structure and duration of the nestlings' begging vocalizations is consistent with results of our earlier study that tested for changes in begging but not non-begging vocalization (chapter 2), and shows that begging signals are not subject to an anti-predator response. Latency until nestlings

gave the first call in response to the contact and provisioning call playbacks depended on the type of alarm call playback. Ground alarm calls led to a longer waiting time until vocalization started than aerial alarm calls and longer, more urgent alarm calls had a similar effect compared to shorter, less urgent alarm calls. It seems likely that the behaviour of the nestlings was still influenced by the playbacks. Nevertheless, the begging response following the provisioning calls was unaffected by the alarm call playbacks. Nestlings did not reduce the intensity of their begging attempt or change the structure of their begging calls in response to the alarm call playbacks.

One explanation for this lack in change of begging calls is that the presence of the parent at the nest signals a predator free environment (chapter 2). In all trials the first calls that nestlings gave upon hearing parental chips were short and 'peep' like while loud and broad frequency begging calls were only initiated when the provisioning calls were played. It is thus most likely that the parental provisioning calls function as an 'all clear' signal. In a recent study on provisioning calls of the black-capped chickadee, *Parus atricapillus*, Clemmons (1995) suggested that provisioning calls release nestlings out of a locomotor inhibition. Adult scrubwrens take great care when approaching a nest with food that no predator is in the direct vicinity. For the small green bee-eater, *Merops orientalis*, Watve *et al.* (2002) were able to show that adults adapt their nest approach according to the direction of gaze of a potential predator (human) that is close to the nest. This indicates that parent birds can use information about predator presence in the nest environment and the predator's potential behaviour to avoid betraying the nest. Our results strongly suggest that parental behaviour can resolve the conflict between signalling and predation for nestling begging.

LITERATURE

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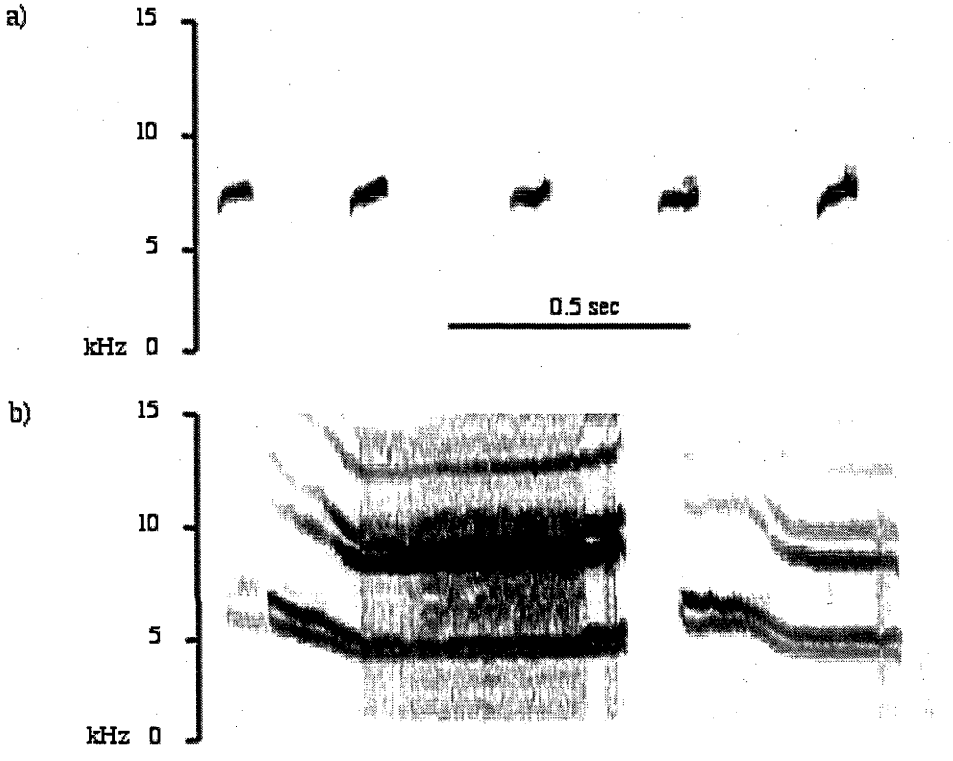


Figure 1: Spectrograms of nestling vocalization. (a) Nestling 'peeps' that are used during non-begging vocalization. (b) Nestling 'whines' that are used as begging calls during a parental feeding visit.

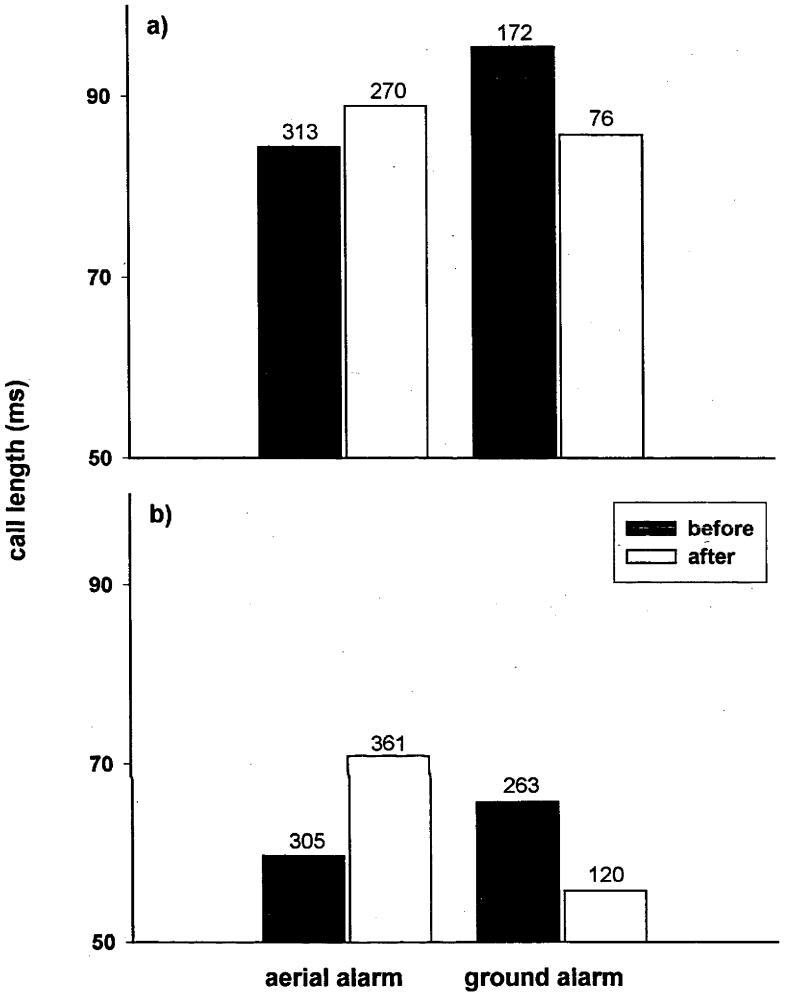


Figure 2: The mean length of nestling calls before and after hearing aerial and ground alarm call playbacks. (a) Response of 5 day old nestlings. (b) Response of 11 day old nestlings. Bars show means estimated from a mixed model and numbers on top of bars represent the numbers of measured calls in this group. The scale of the y-axis is similar for both graphs and was chosen to illustrate the age related changes.

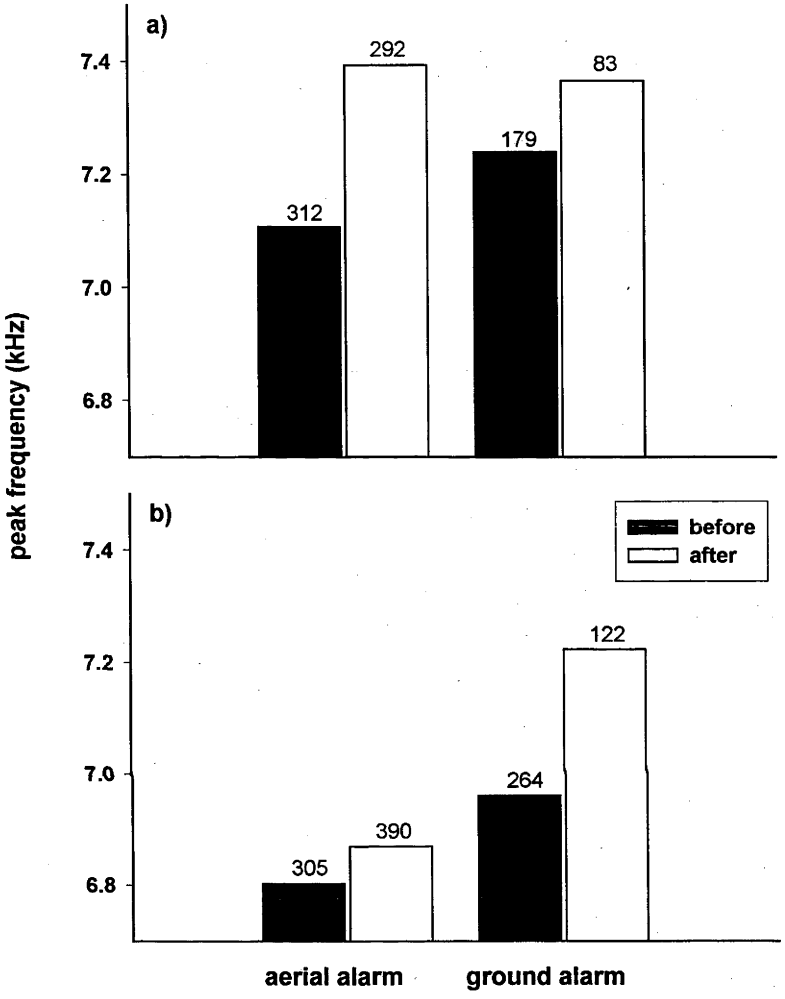
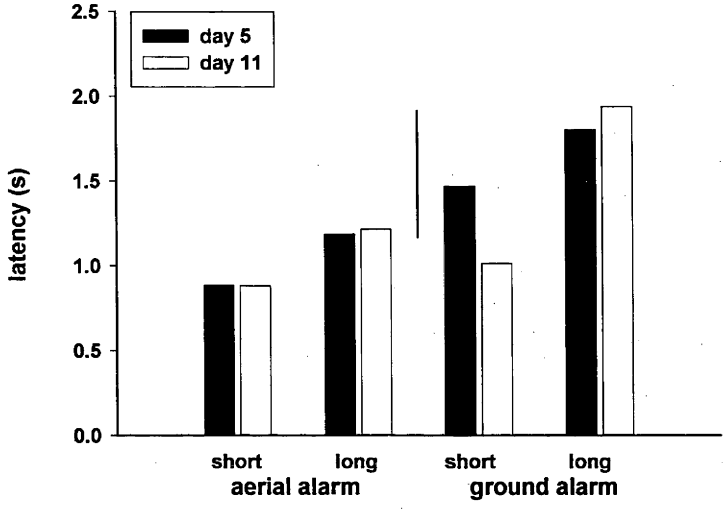


Figure 3: The mean peak frequencies of nestling calls before and after hearing aerial and ground alarm call playbacks. (a) Response of 5 day old nestlings. (b) Response of 11 day old nestlings. Bars show means estimated from a mixed model and numbers on top of bars represent the numbers of measured calls in this group. The scale of the y-axis is similar for both graphs and was chosen to illustrate the age related changes.

a)



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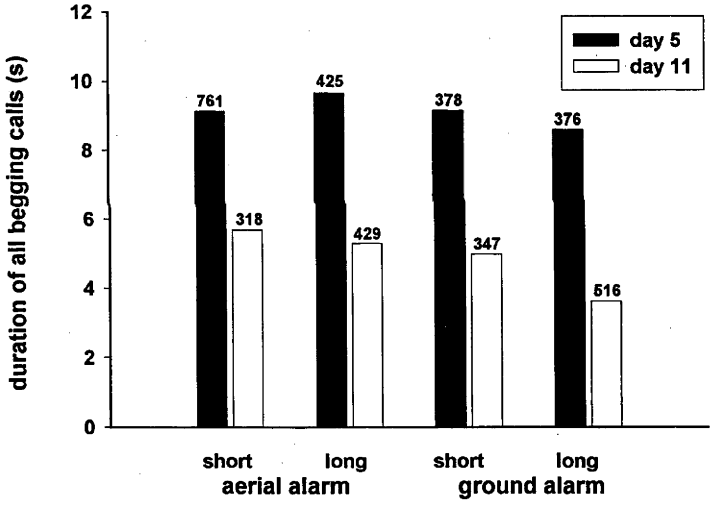

Figure 4: The begging response of the nestlings after hearing a contact and provisioning call playback. (a) Latency until nestlings give their first call measured from the first contact call of the playback. (b) The cumulative duration of all calls given in response to the contact and provisioning call playback. Bars show means estimated from a mixed model. Numbers on top of bars represent the number of measured calls in that group.

Complex signals for a simple task: The provisioning calls of white-browed scrubwrens

Chapter 5

The use of provisioning calls has been described in a variety of altricial and precocial bird species and their main function is thought to be the stimulation of unresponsive nestlings, especially in the first days after hatching. If this is correct, signal design would only be subject to limited constraints, and indeed the provisioning calls of several species have been described as structurally simple. Alternatively, provisioning calls might be used to enable the young to identify their parents after fledging, in which case calls need to be more complex. Another explanation is that parents may use provisioning calls to prompt all nestlings to beg and so provide parents with more information. No current hypothesis can explain a very high level of signal complexity or diversity. Here I describe the provisioning calls of the white-browed scrubwren, *Sericornis frontalis*, and present data from sound recordings of feeding visits over three consecutive seasons. Adults use provisioning calls that have an extremely high level of structural complexity and comprise a large number of distinct call elements. Many of these elements are similar to calls used in the species-specific song and social repertoire. Despite the high grade of complexity, adults use the calls during feeding visits in ways similar to other species that use structurally simpler calls. Call rates go down as nestlings get older and learn to use other cues to identify a landing adult, and calling behaviour depends on the nestlings' begging response. Although these results suggest that scrubwrens use provisioning calls to stimulate unresponsive nestlings, the extreme signal complexity and the frequent use of provisioning calls when nestlings are already begging indicate that other functions might be relevant. I propose several new, not mutually exclusive hypotheses that explain structural complexity in provisioning calls and discuss their relevance to scrubwrens.

1. INTRODUCTION

The size and complexity of a signal are determined by its context, efficacy and cost (Dawkins 1993). A conflict between sender and receiver is likely to increase signal size as well as complexity while signals that benefit both parties are likely to be simple. More intense but not complex signals are required when environmental effects like degradation influence signal transfer, and signalling costs limit size and complexity (Dawkins 1993). The signalling processes between parent birds and their young during feeding events are, due to the close proximity of sender and receiver, under little influence of environmental degradation (but see Horn & Leonard 2002). Studies on signal design have thus mainly focused on potential conflicts and costs to explain the evolution of the apparently unnecessary exaggeration of nestling begging (Wright & Leonard 2002). The acoustic signals that parents use to stimulate nestling begging, provisioning calls, have attracted comparatively little attention. Although the lack of environmental effects potentially allows for complex signals, it is thought that beneficial effects for adults as well as nestlings and the simplicity of the transferred information should lead to a low level of signal size and complexity. Consistent with this view provisioning calls have been described as structurally simple (Clemmons 1997). Nevertheless, there are several examples of at least some structural complexity (Sieber 1985; Lessells et al. 1995; Leonard et al. 1997a). High levels of signal complexity in provisioning calls would require new explanations and hypotheses. The provisioning calls of the white-browed scrubwren that are described and analysed in this chapter are the first example of high structural complexity in this group of vocal signals. In the following paragraphs I will summarize the current hypotheses on the use and structure of provisioning calls and then outline the scope of this study.

Function of provisioning calls

Facilitation of feeding: Provisioning calls are thought to facilitate feeding in the first days after hatching while the young are unable to interact efficiently with feeding adults (Kuhlmann 1909; Bengtsson & Ryden 1981; Khayutin 1985). Very young nestlings are poor at detecting the arrival of an adult, and their ability to actively take up food is not well developed (Kuhlmann 1909; Bengtsson & Ryden 1981; Khayutin 1985; Buitron & Nuechterlein 1993). These skills develop within the first days of life and the proportion of parental feeding visits with provisioning calls, as well as the number of

calls that are given each visit, decrease in many species as nestlings get older (Kuhlmann 1909; Bengtsson & Ryden 1981; Khayutin 1985; Sieber 1985; Buitron & Nuechterlein 1993; Clemmons 1995; Leonard et al. 1997a; Grieco 2001). Similarly the overall length of parental visits declines with increasing nestling age, which potentially indicates an increase in efficiency (Leonard et al. 1997a). This change in parental activity is likely to be caused by the development of the nestlings' responsiveness to stimuli associated with the arriving parent. Nestlings become increasingly responsive to tactile and acoustic signals related to the parent landing at the nest, and respond to changes in ambient light or the silhouette of the parent after their eyes open (Bengtsson & Ryden 1981; Khayutin 1985). In many species, however, parents never completely stop to use provisioning calls when nestlings get older (Clemmons 1995; Lessells et al. 1995; Leonard et al. 1997a).

Parent-offspring recognition: In species where the use of provisioning calls is not restricted to the first days after hatching, provisioning calls might facilitate parent offspring recognition. The young of many colonial species acquire the ability to distinguish their parents from other colony members before they leave the nest (Beecher 1991; Searby et al. 2004). Evidence for a possible use of provisioning calls in this context comes from bank swallows, *Riparia riparia*, and European bee eaters, *Merops apiaster* (Sieber 1985; Lessells et al. 1995). The correct identification of adults minimizes the chance of energetically costly but unsuccessful solicitation attempts, or even attacks from unrelated adults due to misdirected begging (Sieber 1985; Beecher et al. 1985; Lessells et al. 1995; Leonard et al. 1997b).

Acquisition of information: The observation that provisioning calls are more likely to be used when nestlings are reluctant to beg, even when they get older, has lead to the idea that these calls are used to gain information from the nestlings (Bengtsson & Ryden 1981; Leonard et al. 1997a). Nestling begging can transfer information on hunger state, condition and health from an increased begging activity of their young (Kilner 2002; Sacchi et al. 2002; Saino et al. 2003). Adults potentially seek information that helps them to optimize their investment in the young. If this is true, adults should use provisioning calls even if some young are already begging (Leonard et al. 1997a). Consistent with the idea that adults gather information, Khayutin (1985) found that in three species of passerines, pied flycatchers *Ficedula hypoleuca*, great tits *Parus major* and redstarts *Phoenicurus phoenicurus*, provisioning calls were often given when the nestlings were already begging.

Signal design

Many provisioning calls have a simple structural design and no species has been reported to use more than one call type. In black-capped chickadees, *Parus attricapillus*, the response of the nestlings depends largely on the frequency range of the provisioning call. Younger nestlings responded mainly to low frequency components while older nestlings also responded to high frequency components of the calls (Clemmons 1997). The author suggests that short, simple, broad-frequency calls accommodate best for the changes in nestling responsiveness that are caused by an expanding hearing range. Calls of some of the species that have been studied so far seem to fit this pattern (Khayutin 1985; Buitron & Nuechterlein 1993). Nevertheless, other species use provisioning calls that deviate from this simple pattern. In the laughing gull, *Larus atricilla*, adults use a long pure tone call that has a frequency of below 1 kHz (Beer 1970). European bee-eaters, bank swallows and tree swallows, *Merops apiaster*, use modulated pure tones with a frequency range between 1.5 and 4 kHz (Sieber 1985; Lessells et al. 1995; Leonard et al. 1997a). Also the call of the barn swallow, *Hirundo rustica*, seems to have a limited frequency range around 3-5 kHz and a pure tone structure (Sacchi et al. 2002). Recognition of individual parents by nestlings has been shown for all of these species except the barn swallow and most of them are colonial or semi-colonial breeders.

Structurally richer call features like the ones used in these species have been shown to facilitate individual recognition of adults by nestlings (Beecher et al. 1985). This is an indication that the structure of provisioning calls is not only determined by the sensory capacities of the nestlings but by the function they have. If provisioning calls are used for more than simply facilitating feeding, structural complexity should be more common.

Provisioning calls in the white-browed scrubwren

Limited information on the white-browed scrubwren indicates that the provisioning calls used in this species have a complex spectrotemporal structure (Higgins & Peter 2002), but no study has analysed the design or function of these calls. Here I present the first quantitative and qualitative description of an avian provisioning call system with a high level of structural complexity and a diversity of call types. The aim of this study is to: (1) describe the complexity and diversity of scrubwren provisioning calls; (2) analyse their use and compare it with results from other species;

and (3) test predictions from established as well as new hypotheses on the use and design of these calls (chapter 1).

I will test the following predictions from the three main hypotheses on the use and design of provisioning calls. (1) If provisioning calls facilitate feeding in the first days after hatching, the rate of visits with provisioning calls should decline. Adults should not call when nestlings are already begging and provisioning calls should not be used when nestlings get older. Nestlings should develop the ability to respond to the arrival of an adult independent of provisioning calls, and calls should be of simple structure. (2) If provisioning calls are used to facilitate identification of adults, the rate of calling should be independent of the ability of the young to respond to an arriving adult, and calls should have structural features that make discrimination between individuals possible. (3) If provisioning calls are used to gain information for decisions on provisioning, adults should use provisioning calls if nestlings show no or low levels of begging activity even when nestlings get older. Adults should also call when only one nestling is begging. The number of calls should vary with nestling activity. The signal design should ensure a high level of stimulation of the nestlings but does not need to show high levels of individual variation within a population.

2. METHODS

(a) Study species

The white-browed scrubwren is a cooperatively breeding passerine endemic to Australia. Breeding groups consist of one female, one dominant male and one or several male helpers (Magrath 2001). Scrubwrens prefer habitats with thick understorey in which territories are communally defended throughout the year. The female builds the dome-shaped nest on or near the ground in well concealed locations, under leaf-litter or in large grass tussocks. Nest predation is intense and females can lay up to six clutches in one season if depredation is high (Magrath et al. 2000). Average clutch size is three eggs that are laid at two-day intervals. In most clutches the young hatch within several hours and the average length of the nestling period is 15 days (Magrath et al. 2000). Females brood the nestlings with decreasing intensity during the first two to three days after hatching. The dominant pair and often subordinates feed the nestlings regularly until fledging (Magrath & Whittingham 1997). Brood division occurs in most broods from the second week after fledging (Leedman & Magrath 2003). Adult mortality is low and adults can stay for more than 15 years in one territory.

Adult scrubwrens have a rich vocal communication system that is used to facilitate contact within the group and interactions with neighbouring groups. Vocal signals of known function are male songs that are used for territory defence (Ansell 2004), contact, pattern and flight calls used in social interactions within groups, aggressive calls used in territorial interactions with neighbouring groups, nest prospecting calls, female begging calls that are used when soliciting allofeeding from a male, and two types of alarm calls that warn of aerial and ground predators (Higgins & Peter 2002; Leavesley & Magrath in press). Vocalizations of unknown function include female song, which is similar to male song but occurs rarely, and low amplitude sub-song that can be performed by both sexes (Platzen unpubl.).

When an adult approaches a nest with food it normally perches away from the nest before it flies straight into the vegetation covering the nest entrance. While perched the adult is presumably scanning the nest environment for predators that might observe the approach. During the process of approaching the nest the adult often gives contact calls ('chips') that are similar to calls used in other social contexts and are potentially directed to nestlings as well as other group members. Upon leaving the nest, adults are normally silent until they perch away from the nest. During feeding visits by the adults, scubwren nestlings vocalize with long, broad frequency begging calls ('whines', see

chapter 4). Due to the enclosed nature of the nest, quantitative observations of begging behaviour aside from calls are not available. Nevertheless, preliminary video observations at two nests indicate that begging calls are in almost all cases connected to gaping and orientation of the head to the nest entrance (Platzen unpubl.). In between feeding visits nestlings vocalize with 'peeps', which are short high-pitched calls of lower amplitude than the begging calls (Maurer et al. 2003). Peeps occur regularly, and can involve only one or more of the nestlings at a time (Platzen unpubl.). When peeping, nestlings do not gape or orient towards the nest entrance. They typically call with their bill closed and remain lying on the nest floor (Maurer, Platzen unpubl.).

(b) Sound recordings

I recorded 456 feeding visits during the 2001, 2002 and 2003 breeding seasons at 45 different nests. Sample sizes for the different nestling ages are shown in figure 1. The data include 175 feeding visits by females, 226 by dominant males and 38 feeding visits by subordinate males. Recordings were made onto a Sony TCD-D100 DAT recorder at 44.1 kHz sampling frequency with Audio Technica ATM15a condenser lapel microphones. The microphones were attached to a small branch and placed 16 cm away from each nest facing the entrance. A distance marker made out of green wire that extended outwards from the lower rim of the entrance was placed at each nest after the female had started incubating. A fake microphone was left permanently in position, together with the distance marker, to avoid aversive reactions during the recordings due to a new object close to the nest. All nests were covered with a mesh wire cage that allowed the adults to visit the nest but excluded predators. During the recordings I observed the nests and noted the identity of feeding adults.

Recordings were digitally transferred onto a Macintosh computer and analysed using spectrograms with a filter bandwidth of 1399 Hz, a frame length of 128 points and the grid resolution set to 43.07 Hz and 0.726 ms in Canary 1.2.4. (Charif et al. 1995). For all adult calls given during a feeding visit I measured the call length, the minimum, maximum and peak frequencies, and the amplitude. The data collection focused furthermore on (1) the vocal behaviour of the nestlings at the time of arrival of the adult, (2) the calling behaviour of the adult, and (3) the subsequent response of the nestlings to adult calls. To test whether the nestling activity at the time of landing had any influence on the behaviour of the adult I recorded whether the nestlings were silent, peeping or whining before the adult uttered any provisioning calls. For the adult I recorded the

overall length of the feeding visit, whether provisioning calls were given or not, the length of the calling bout, the cumulative length of all calls given as a measure of sound output, and the type and number of all calls. To test whether the response of the nestlings had any influence on the adult behaviour I recorded whether the nestlings were peeping or whining, including the intensity of the whines, after the adult gave a provisioning call. I included the nestlings' response to the provisioning calls in the analyses because in most cases it overlapped with the adult's calling activity and I assumed that the adults could adjust their calling activity according to the nestlings' behaviour. Only during 3 visits did the nestlings stay completely silent and these nests were excluded from all analyses that contained the nestlings' response.

(c) Statistical analysis

Analysis of feeding visits: I omitted 17 of the field recordings from the analyses because the adults gave unusually long provisioning calls, probably due to disturbances near the nest preceding the feeding visit. The data set that contained the remaining 439 visits was unbalanced because nests as well as adults were repeatedly sampled and most variables had missing data, due to technical difficulties or lack of information. I therefore used a Mixed Model approach with restricted maximum likelihood estimation (REML) in Genstat 5 (release 4.2, Genstat-Committee 2000) for the analyses. Initial models contained a nest identifier and an adult identifier nested within the nest identifier as random effects, to control for variance between nests and variance between adults within nests. Variance components of random effects were estimated using the REML procedure in GENSTAT and for most models the adult identifier was dropped, as it did not show any effect. There was no effect of year in any analysis and it was dropped from all final models. All binary dependent variables were analysed with a Generalized Linear Mixed Model (GLMM) and the reported probabilities are estimates from the models. The significance of each fixed effect was assessed using Wald statistics when the effect was last in the model. Continuous dependent variables were analysed using Linear Mixed Models (LMM) and all reported relationships are estimated from the models. I used the sub-model routine implemented in Genstat (Genstat-Committee 2000) to assess the significance of the fixed effects in the LMMs, by calculating the change in deviance caused by dropping a fixed effect from a full model that contained all significant effects. All continuous dependent variables were transformed with a

natural logarithm prior analysis. Residuals did not deviate significantly from a normal distribution in any model.

The following fixed effects were used in all models. Due to the social system of the scrubwren 38 of the feeding visits were from subordinate males and I tested a factor that encoded for female, dominant male and subordinate separately. I furthermore included the number of nestlings and the age of the nestlings as fixed effects. Due to the uneven spread of recordings during the nestling stage (figure 1), age was encoded as a factor with 6 levels (nestling age day 2 and day 3 = level 1; days 4 + 5 = 2, days 6 + 7 = 3; days 8 + 9 = 4; days 10 + 11 = 5; days 12 + 13 + 14 = 6). In the models that contained adult behaviour as a dependent variable I included the nestlings' initial activity at the time of landing encoded as silent, peeping or whining. The response of the nestlings to the calls of the adult was encoded as either peeping or whining. As the whines that the nestlings produced varied greatly in intensity I created a variable that included peeping, whining and a third factor level for all visits that contained whines intense enough to produce non-linear phenomena. Non-linear phenomena like the deterministic chaos observed in intense nestling begging can be a sign of increased arousal and make a call harder to ignore for the receiver (Fitch et al. 2002). I kept this factor in the model instead of the two level response variable whenever it showed significant differences between low intensity and high intensity whining. All second order interactions were included and only significant effects are reported in the results section. The presented observed means and standard errors vary in many figures from the model estimates because the statistical models account for effects of repeatedly sampled individuals and unevenly distributed data.

3. RESULTS

The results section is separated into two parts, (a) the description of call diversity and (b) the analysis of nestling and adult behaviour during the feeding visits. Throughout the results section I will refer to the complete set of elements given during one visit as one 'call', and to distinct sub-structures of a call that are separated by a silent interval as 'elements'.

(a) Description of provisioning calls

General description

The provisioning calls used by adult scrubwrens during feeding visits were structurally variable and potentially represented a large number of distinct element types. They were typically given in a string of call elements with short inter-element distances (figure 2). Usually the calls were given as soon as the adult reached the nest entrance and although visual observations of the recorded feeding events were not possible, it seems likely that the provisioning calls preceded the actual feeding. Adults gave a second bout of provisioning calls that was separated from the initial bout by more than two seconds in less than 10% of all visits containing provisioning calls (30 out of 362) and in extreme cases calling continued for more than 10 seconds (n = 17). These events were mostly connected to disturbance at the nests before the feeding visit or to nestlings being silent and unresponsive over the course of several feeding visits. The number of call elements used during one visit ranged from 0 to more than 300 and the overall mean was 15.5 calls ± 25.8 s.d. (figure 3).

Element types

The vast majority of calls contained one or both of two types of call elements that together accounted for 75% of the 7085 recorded call elements (figure 4a, b). The first accounted for 4275 of all elements and the second for 457 elements. A typical string of call elements consisted of several repetitions of either of these two types in which other call elements were embedded or placed at the beginning or end (figure 2). As these two element types were used almost invariably when provisioning calls were given and were structurally uniform, I label them the 'basic' type. The mean length of

basic elements was 23.1 ms ± 0.18 s.e.m. (figure 5a), and the mean peak frequency of the basic elements was 6.4 kHz ± 0.04 s.e.m. (figure 5b).

The remaining 2353 elements were grouped as 'complex' type because many of them had a more intricate structure than the basic elements. The mean length of complex elements was 67.6 ms ± 1.7 s.e.m. (figure 6a), and the mean peak frequency of complex elements was 4.8 kHz ± 0.04 s.e.m. (figure 6b). Overall, they were more structurally variable than basic call elements and were on average longer and had lower peak frequencies (length t-test: $t = 14.62$, $p < 0.001$; peak frequency: $t = 22.45$, $p < 0.001$). Besides elements that could be identified as originating from the species-specific repertoire or were imitations of other species (see below), adults used a variety of elements that could not be identified and might not be used in any other context (figure 7). A further classification of complex call elements and the establishing of individual repertoires was attempted, but proved to be arbitrary and impossible to verify. As the only response to all calls was an increase in nestling vocalization, no functional differences were available to compare groups of elements. An initial grouping process established 111 different element types but this can only be viewed as a rough estimate of how many types were present.

Origin of complex call elements

(a) Songs: Many of the call elements used by adults were similar to vocalizations used in other social contexts. The main source of provisioning call elements seemed to be adult song. I compared the recordings of the feeding visits with material from a recent study on male song in the study population (Ansell 2004) and found 28 elements that were similar to song elements or to introductory elements of songs (figure 8). Song-like elements were used by males and females alike. As the sample of known songs was restricted to a sub-sample of males in the 2003 season, but the recordings of feeding visits were made at nests of a larger sample of males as well as females from 2001 to 2003, it seems likely that the number of provisioning call elements used in male or female song is higher. Very rarely some of the adults used several repetitions of two elements that resembled scrubwren song except that the element combinations did not represent known song syllables. Figure 9 shows the four examples that were found. In all cases one of the elements in each syllable has been found in songs from the study area but the other has not been previously described as song component. These two-element combinations are thus likely to represent song

syllable types that have not been recorded up to now, an indication that there could be more than 28 song elements in the provisioning call repertoire.

(b) Adult social calls: Other call elements resemble calls that are used in adult social interactions. Figure 10a shows call elements that are similar to an adult 'chip', a contact call that is used in a wide variety of contexts. It can be used during group movement as well as close interactions within a group and it is one of several calls that are used during the approach to a nest during a feeding visit. The calls shown in the spectrogram were given in quick repetition and in connection with other provisioning calls while the adult was inside the nest. Another call element found in provisioning calls is used during group interactions as part of the so called 'pattern calls' (figure 10b). These calls can also be used during the nest approach. Figure 10c shows elements that resemble aerial alarm 'trills' (chapter 3), except that they were given while the adult was inside the nest and in connection with other provisioning calls. It is thus highly unlikely that they were given as a warning signal. One adult also used elements similar to nestling vocalizations. The call element in figure 10d appears to be a short and low frequency imitation of a nestling begging call (see chapter 4 for a nestling whine).

(c) Mimetic elements: In addition to calls that were species specific, adults also produced imitations of other bird species. The most common imitation was of the yellow-rumped thornbill song, *Acanthiza chrysorrhoa*, which is also a song pattern used by several males of the population (figure 11a). Another imitation of a yellow-rumped thornbill call, which was used by one adult at the nest, has not been found in any of the known songs (figure 11b). Another imitation that has not been described before for scrubwrens, was that of a striated pardalote call, *Pardalotus striatus*, which was used during only one feeding visit but was repeated twice with high accuracy (figure 11c). Consistent repetitions of element combinations were extremely rare and only two additional multi-element combinations that were repeated twice by the same bird were found (one is displayed in figure 11d). These combinations might represent imitations of other bird species but have not yet been identified.

(d) Elements of unknown origin: The majority of complex call elements (65% of 2353) could not be identified as belonging to any of the described groups (figure 7). Parts of this large group are many short and unmodulated elements but also the longest element type found. How many of these call elements belong to the song and social repertoire of scrubwrens remains to be shown.

(e) Calls not used as provisioning calls: One element type was used during feeding visits but is unlikely to function as a provisioning call. It was only given by females when brooding newly hatched young. Females can brood the young for several days after hatching and when a male approached the nest with food during that time, females often uttered a long string of low frequency elements. It is thus likely that this element type is used to coordinate the adult interaction rather than being addressed to the nestlings. This element type was excluded from all analyses. It is also used in a wide variety of other social contexts. Outside of the nest this and similar element types are used as prospecting calls while male and female search for a nest site, and during aggressive encounters with other groups.

Variability of call elements

One of the reasons why a classification into distinct element types proved to be very difficult was that even calls obviously belonging to a certain group displayed a very high variability in their time and frequency structure. This variability was apparent on the population as well as individual level. Even when elements of a specific type were used they were often given quite differently on different occasions or displayed structural variability within one call bout. The two main mechanisms leading to variability in call design that could be identified from the data set were (a) the usage of intermediate element structures and (b) the fragmentation of larger elements into small pieces or composition of larger elements from small pieces.

(a) Use of intermediates: On a few rare occasions adults displayed the transition from one element type to another within one call bout, during which they used intermediate call elements that showed structural features in between the two endpoints (figure 12a-c). Although obvious transitions were an exception, many of the call elements that were used independently and together with other non-similar elements revealed intermediate structures. Figure 12d displays 6 elements that were taken from different individuals but lie on a continuum. Similar features were apparent in the majority of elements. Figure 8d shows that an element that is used in a very stereotyped manner in songs is produced with high variability when used in provisioning calls. The first element in this sequence contains an added segment while the last elements are successively shortened.

(b) Fragmented or composed elements: The fragmentation of larger elements was obvious, when the resulting fragments were kept in the original temporal structure

(figure 13). All of the fragments shown in figure 13 resemble call elements found in provisioning calls that did not contain the 'original'. For example, the fragments of the call element shown in figure 13d, an inversion of the song element shown in figure 8a, have been found in the provisioning calls of several individuals that did not display the full element. These elements were used in combination with other structurally unrelated elements. Figure 14 illustrates another case of the independent usage of elements that potentially are derived from a larger element. The 'original' element in figure 14a is a widely used provisioning element type and song element that occurs in many different versions but seems to have a similar structure within each individual. A segmentation that still shows the original temporal pattern (figure 14b) was only displayed by 3 individuals. A double-bow segment is used as part of a song-like syllable (figure 9c) and the single bow elements are widely used with many structural variations and without the original temporal pattern (figure 14c). The half bows shown in figure 14d were only used by one individual but on several occasions. Figure 15 shows a very similar process for calls that are modulated on a lower frequency. Although no other example can be displayed with as much detail it seems likely that similar processes of fragmentation could be used with other elements and lead to the observed large number of highly variable and unidentified provisioning element types. Figure 13c shows an element that is split into three different parts. All three fragments are widely and independently used call elements, and the combination, as seen in the spectrogram, was only displayed by one individual. This illustrates that it is unclear whether the observed processes are fragmentations of 'originals' into smaller pieces or whether the smaller pieces are 'originals' that are used to compose larger units.

(b) Analyses of feeding visits

Vocal behaviour of the nestlings upon arrival of the adult

The likelihood of whining before provisioning calls increased significantly as nestlings got older ($\chi_5^2 = 48.3$, $p < 0.001$; figure 16). Four and 5 day old nestlings gave whine calls before any provisioning call in less than 20% compared to 50% of visits when 10 and 11 days old. The most likely explanation for the unprompted begging calls is that the nestlings reacted to other cues connected to the adult's arrival. Nevertheless, at no age did more than half of the broods respond with whines without being prompted

by provisioning calls. Overall, in 39% of 423 feeding visits nestlings were silent when the adult arrived at the nest and did not vocalize until the adult gave a provisioning call. In 34.5% of cases the nestlings were peeping, and in another 26.5% cases the nestling started to whine before the adult uttered a provisioning call.

The behaviour of the adult

(a) Duration of the feeding visit: The time that an adult spent at the nest from landing to take off was primarily influenced by the age of the nestlings and the vocal activity that the nestlings displayed when the adult landed. Feeding visits got shorter when nestlings got older but were longest when the nestlings were peeping before the adult called (nestling age: $\chi_5^2 = 85.9$, $p < 0.001$, figure 17a; nestling activity: $\chi_2^2 = 16.4$, $p < 0.001$; figure 17b). The response of the nestlings to the provisioning calls influenced the length of the visit less strongly than the other effects but the visits got slightly shorter when nestlings responded with whines compared to peeps (peeps estimated mean = 14.6 s, whines = 12.2 s; $\chi_1^2 = 5.9$, $p = 0.02$). No difference between intense and less intense whining was detectable.

(b) Likelihood of provisioning calls: The likelihood of giving a provisioning call decreased as nestlings got older and when they were more active (nestling age: $\chi_5^2 = 58.6$, $p < 0.001$; figure 18a; nestling activity: $\chi_2^2 = 59.2 < 0.001$; figure 18b). The adults used provisioning calls in 83.4 % of 434 visits, and overall the likelihood of using provisioning calls was at no age lower than 40%.

(c) Length of call bout: The length of the provisioning call, measured from the beginning of the first to the end of the last call element, decreased when nestlings responded with whines and was and was even shorter with high intensity whines ($\chi_2^2 = 52.6$, $p < 0.001$; figure 19a). The length of the call also depended on who fed the nestlings; subordinates called significantly longer than the dominant pair ($\chi_2^2 = 18.7$, $p < 0.001$; figure 19b).

(d) Sound output: Sound output was measured as the cumulative length of all provisioning call elements given. For visits where the exact length of the basic call elements was not measured I calculated the length of all basic elements within one call bout as number of calls multiplied by the mean basic element length. Sound output during a bout was influenced by other factors than the bout length. Sound output decreased with nestling age when nestlings responded with whines and increased with

nestling age when nestlings did not whine (nestling age: $\chi_5^2 = 36.3$, $p < 0.001$; nestling response: $\chi_1^2 = 26.3$, $p < 0.001$; nestling age*nestling response: $\chi_4^2 = 9.1$, $p = 0.06$; figure 20). The intensity of nestling whines did not influence the adult sound output. Similar to the bout length, adult sound output was higher for subordinates than for the dominant pair ($\chi_2^2 = 6.7$, $p = 0.04$; figure 21).

(e) Use of complex elements: Adults used only the basic element types in 39 % of 362 visits and basic as well as complex elements in 58 % visits. Only 3 % of feeding visits contained complex but no basic element types. The likelihood that complex element types were used by an adult declined with nestling age and the nestlings' activity at the time of landing (nestling age: $\chi_5^2 = 60.0$, $p < 0.001$; nestling activity: $\chi_2^2 = 19.8$, $p < 0.001$; figure 22a). When the nestlings were silent upon the arrival of the adult the use of complex provisioning calls was significantly more likely than when they were peeping or whining (figure 22a).

Summary of results: Overall, the duration of feeding visits and the use and length of provisioning calls decreased when nestlings were more responsive and subordinates called more intensely than the dominant pair (table 1).

4. DISCUSSION

The provisioning calls of white-browed scrubwren adults showed a degree of structural complexity that has not been described in any other species. Complexity was achieved by the use of a large number of distinct element types as well as high variability within types caused by the use of intermediate call elements and fragmented / composed calls. Despite this difference in call structure from provisioning calls of other species the usage of the calls followed the pattern that has been described for many other species (Kuhlmann 1909; Bengtsson & Ryden 1981; Khayutin 1985; Buitron & Nuechterlein 1993). As nestlings got older, the rate of visits with provisioning calls as well as the sound output per visit decreased. The probability of unprompted nestling begging increased with age, indicating a developing ability to react to stimuli related to an approaching adult other than provisioning calls. Adults responded to a lack of nestling begging activity by increasing their calling activity. The results thus support the hypothesis that provisioning calls are used to facilitate feeding mainly in younger nestlings. Nevertheless, provisioning calls were used in 50% of the visits in older nestlings as well as in a high proportion of visits when one or more young were begging when the adult landed. The high structural complexity, long calling bouts and the use in broods with older nestlings indicate that other factors influence function and signal design as well.

(1) Facilitation of feeding: Most of the results support the hypothesis that adults use the provisioning calls to increase the efficiency of nestling feeding. Call rates declined as nestlings got older and developed the ability to respond to the approaching adult without vocal stimulation. Furthermore, adult calling behaviour was tightly linked to the response of the nestlings. The likelihood of calling increased when the nestlings were unresponsive upon the arrival of an adult and the duration of a calling bout as well as the sound output increased when the nestlings did not respond with begging. The use of complex provisioning calls decreased as nestlings got older and was also linked to the nestling activity upon landing. Similar results have been observed in several other species (Bengtsson & Ryden 1981; Khayutin 1985; Buitron & Nuechterlein 1993; Clemmons 1995; Leonard et al. 1997a).

The facilitation of feeding hypothesis is also supported by other results and observations. Subordinate males showed a higher calling activity than the dominant pair. The subordinates in the data set were not older than two years. It seems likely that

lack of experience could result in a less efficient adult-nestling interaction so that the subordinates tried to improve by an increased use of provisioning calls. A comparison with young unexperienced females could help to answer the question of whether experience is a factor influencing the use of provisioning calls. Unfortunately this is hampered by the fact that the age of most females is unknown because they are the dispersing sex. Casual observations of adult allofeeding, the provisioning of the gravid female by males of the group, show that males sometimes use provisioning calls before feeding if the female is not responsive (Platzen unpubl.). Provisioning calls thus seem to have a generally stimulating effect during feeding interactions even in adults. All these results show that facilitation of feeding is one of the main functions of the provisioning calls but they do not explain the complex signal design. Results of other species indicate that much simpler signals can have a similar stimulating effect (Khayutin 1985; Clemmons 1995; Clemmons 1997; Leonard et al. 1997a). Unless the feeding interaction between scrubwren adults and nestlings is particularly difficult or scrubwren nestlings are much less responsive than young of other species, it seems unlikely that a mere increase of responsiveness is the sole purpose of these signals.

(2) Parent-offspring recognition: Another possible explanation for the observed complexity in call structure is that provisioning calls facilitate the identification of individual adults. Brood division occurs in most scrubwren broods from the second week after fledging (Leedman & Magrath 2003). Even in undivided broods and single fledglings, individual young are almost exclusively fed by a single adult. Fledglings potentially play an active role in maintaining brood division and choose a feeding adult, with dominant fledglings often monopolizing the best feeder (Leedman & Magrath 2003). Adults might favour brood division as well, to reduce the effects of sibling competition (Harper 1985). It seems that a mechanism that enables young to identify individual adults by their calls by the time of fledging, as it has been described for other species (Sieber 1985; Lessells et al. 1995; Leonard et al. 1997b), would have several benefits. Nevertheless, the observations of adult feeding visits did not support the prediction that provisioning calls are used until the end of the nestling period and independent of nestling activity. Calling activity in the last days before fledging was low compared to the first days after hatching and adults responded to nestling begging with low rates of provisioning calls. The extreme variability of calls also seems to act against a function as a discriminating tool. Nestlings were unlikely to hear the same calls from one adult in high repetition and very rarely would hear the same sequence of

call elements. All species studied so far display a single call type that has an individual signature (Sieber 1985; Lessells et al. 1995; Leonard et al. 1997b). It might be possible that instead of individual variation in one call, scrubwren young use differences in frequencies or other structural features within a wide variety of calls to enable identification of individual adults. This hypothesis would only support the differences within adults feeding at one nest but does not explain the extent of variability within the whole population.

(3) Acquisition of information: The high structural complexity of provisioning calls, long calling bouts and large numbers of calls used per visit might be explained by the need of adults to gain more information from their brood than they would get without calling. Adult calling occurred even when nestlings got older and more responsive, and calling bouts were longer when nestlings responded with low intensity whines compared to high intensity whines. This behaviour indicates that in some instances although the nestlings were begging their response was not sufficient. Nestling begging displays are complex multi-component signals that can transfer information about hunger state, condition and health to the feeding adult (Kilner 2002; Sacchi et al. 2002; Saino et al. 2003). Adults have been shown to use this information to adjust their feeding effort (Ottosson et al. 1997; Saino et al. 2000; Leonard & Horn 2001a). Furthermore, the observed complex signal design is in agreement with the prediction of a strong stimulating effect of the signals used. Adults potentially use the wide range of call elements from their social repertoire to take advantage of an existing receiver bias in their young (Guilford & Dawkins 1991; Dawkins 1993). The young of many species have a predisposition to respond to the acoustic signals that are specific to their species (Baptista 1996). The use of a wide range of song elements as well as other calls used in the context of group interactions might thus increase the effectiveness of the adult calls.

Other functions of provisioning calls might explain the observed complexity and variability in signal design better than the three established hypotheses. In the following paragraphs I formulate three new hypotheses, and compare the use and design of scrubwren provisioning calls with their predictions.

(4) Overriding sibling competition: Adults could potentially use provisioning calls to override the effects of sibling competition. As nestling begging often reflects the outcome of sibling competition (McRae et al. 1993; Kacelnik et al. 1995; Ostreiher 1997), adults that feed young preferentially might find themselves in a conflict with

their nestlings about who will be fed. A vast number of theoretical and empirical studies on parent-offspring conflict have shown that the parental provisioning optimum can be different from the optimum of the current brood (Godfray & Parker 1992; Mock & Forbes 1992; Godfray 1995; Kilner & Johnstone 1997; Budden & Wright 2001a). During every feeding visit the parental provisioning optimum can be different from the optimum of the most dominant or most intensively begging nestling (Lessells 2002). In other words, if the outcome of sibling competition is different than the adult's current feeding optimum, adults might choose to feed a nestling of their choice instead of following the nestlings' 'choice'. For example in crimson rosellas, *Platycercus elegans*, adults control food allocation and do not necessarily feed the nestling that begs the most (Krebs et al. 1999; Krebs & Magrath 2000).

The necessity for parents to counteract sibling competition should be more pronounced when adults are restricted in their choice of who to feed by the nestlings' activity. This may be caused by the nest structure if, for example, nestlings in burrow nests or dome-shaped nests have the possibility to exclude their siblings from the optimal feeding position. Several different scenarios of adult-nestling interaction are possible. Firstly, if dominant nestlings have the opportunity to successfully prevent their siblings from begging and the adult provisioning optimum is different from the optimum of the dominant nestling(s), adults could choose to call until a weaker nestling has the chance to get itself into position to be fed. Secondly, if sibling competition is decided by hunger state and the adult's optimum is not to invest into the hungriest nestling, adults could call until a less hungry nestling that represents their optimal choice gets itself into position to be fed. This could also mean that the adults' feeding decisions are based on previous feeding events and not only on the current status of the brood. To achieve the stimulation of previously unresponsive or 'unavailable' nestlings, adults should use acoustic signals that have a strong impact on the nestlings. This could potentially explain the use of structurally complex and long provisioning calls.

Predictions: This hypothesis is tightly linked to the acquisition of information hypothesis but states that parents seek to stimulate particular nestlings whenever their feeding optimum does not comply with the outcome of sibling competition. It requires that adults have provisioning rules other than merely feeding the nestling that begs most or is closest to the adult. Adults should also be restricted in their freedom to choose their preferred nestling by sibling competition, potentially by the structure of the nest. This mechanism may be more important in species with burrow, cavity or dome shaped

nests. It might also be enhanced by hatching asynchrony and resulting increased levels of sibling competition. Predictions are similar to the ones stated for the gain of information hypothesis. One distinction is that the acquisition of information hypothesis predicts that adults take only the current state of the brood into account while for the overriding sibling competition hypothesis the feeding history of each nestling might be of importance. Provisioning calls should be used when nestlings get older, if the influence of sibling competition remains high, and the signal design should be conspicuous and stimulating for all nestlings.

Similar to the acquisition of information hypothesis, the overriding sibling competition hypothesis is supported by the high variability of call elements and the large number of social call elements. A resulting intense stimulation of nestlings could increase the control that adults have over the allocation of food. Also the high rate of provisioning calls during visits where nestlings were begging without being prompted is in accordance with the predictions. The feeding visits where adults gave a second bout of provisioning calls, although one of the nestlings had already responded with whines, show that adults sometimes hesitated to feed an already begging young. Although the number of these split bouts was low, similar processes could have occurred when adults used single long calling bouts. In broods of three, one of the nestlings is often smaller than the other two (Magrath unpubl.). When food supply is limited adults might choose to allocate food preferably to the dominant large nestlings to optimize their investment. When food is abundant, they might choose to allocate food evenly to all nestlings and overcome the dominancy of larger nestlings, as observed in crimson rosellas, *Platycercus elegans* (Krebs & Magrath 2000). The dome-shaped nests often have a reduced accessibility due to their position under leaf litter or in grass tussocks. Video observations show that adults do not enter the nests to feed their young but stand at the nest rim while the nestlings move their heads towards the entrance (Platzen unpubl.). A test of the acquisition of information as well as overriding sibling competition hypothesis requires visual observations of nestling identity and activity during feeding events. This information is currently not available.

(5) Tutoring: This hypothesis predicts that adults use provisioning calls to tutor their nestlings about the species-specific call repertoire. This hypothesis predicts that calls are used throughout the nestling period and are not restricted to the time before the feeding event but could be given at any time during the stay at the nest. The signal design should be similar to the call repertoire of the species and have a low level of

individual variability. As calls that are similar to calls used in adult social interactions would be given independent of their normal function and context, the tutoring process would be limited to the neuronal development of nestlings or a very general learning of call structure rather than function.

The hypothesis that adults tutor the species-specific repertoire to the nestlings is supported by the high rate of song and social call components used in provisioning calls. Nevertheless, other results speak against a tutoring function. Firstly, if calling at the nest is crucial for the vocal development of young then adults could use the time after they have fed their young and give calls. A restriction to the moments before nestlings are fed and the observed relationship between nestling activity and adult calling do not support this hypothesis. Secondly, after fledging the young stay in their natal territory and are exposed to vocalizations of their parents and other group members for a prolonged period of time. Price (1998) showed that the cooperatively breeding stripe-backed wrens, *Campylorhynchus nuchalis*, under similar conditions learn their social call repertoire from same-sex relatives. Thirdly, the use of imitations of bird species other than the ones that are commonly used in adult song seems to be unlikely if the function was to teach young the repertoire of their own species.

(6) Predator avoidance: This hypothesis makes predictions about signal design only. It predicts that adults use provisioning calls that have a highly variable structure to prevent predators from learning to associate a certain call type with the availability of prey. This hypothesis requires the presence of nest predators that hunt by sound and predicts that calling activity should be low when predator density is high and that the signal design should be highly variable to prevent predators from learning.

The imitation of other bird species might lower the risk that provisioning calls are used as cues for nest predators. The large repertoire and variability combined with calls from other social contexts and other species could prevent predators from cueing in on a particular type of call. However, it seems unlikely that predators would have the opportunity to overhear the provisioning calls because adults take great care to scan the nest environment thoroughly before approaching the nest (chapter 4).

Contrary to the predator avoidance hypothesis the usage of a highly diversified repertoire of provisioning calls might even increase the risk of predation. If nestlings respond with begging to a wide range of vocal signals, including calls of other species, the danger of misdirected begging in the absence of an adult increases. Nestling scrubwrens have been observed to react with begging to their own species' song as well

as songs of superb fairy wrens, *Malurus cyaneus*, and the European blackbird, *Turdus merula*, that are given near the nest (Platzen unpubl.). Misdirected begging and other nestling vocalizations in the absence of adults can potentially be overheard by nest predators (Budden & Wright 2001b; Leonard & Horn 2001b). Predation caused by an increased responsiveness of nestlings to wrong stimuli would be a cost that is associated with the use of complex provisioning calls.

Contrary to the current opinion that the design of provisioning calls is generally simple (Clemmons 1997), the provisioning calls of the white-browed scrubwren are of high structural complexity and diversity. The descriptive nature of the data presented in this chapter allows me to formulate hypothesis but not to provide definitive tests of the predictions. It seems likely that provisioning calls facilitate feeding, as in other species. However, adults give provisioning calls even when nestlings are begging and these calls might allow adults to gather information about their brood, possibly to override sibling competition. The extreme variability of calls within individuals makes it unlikely that parent-offspring recognition is the only function. It also appears unlikely that the high variability of calls is an adaptation to avoid overhearing by predators, as adults take great care not to approach a nest when a predator is nearby. Playback experiments as well as video observations are necessary to assess the importance of each one of the hypotheses for the evolution of the seemingly exaggerated signal complexity in scrubwren provisioning calls. It seems unlikely that complex provisioning calls are a phenomenon that is restricted to scrubwrens and more information about other provisioning call systems is needed to establish whether the hypothesized processes influence signal design in other species.

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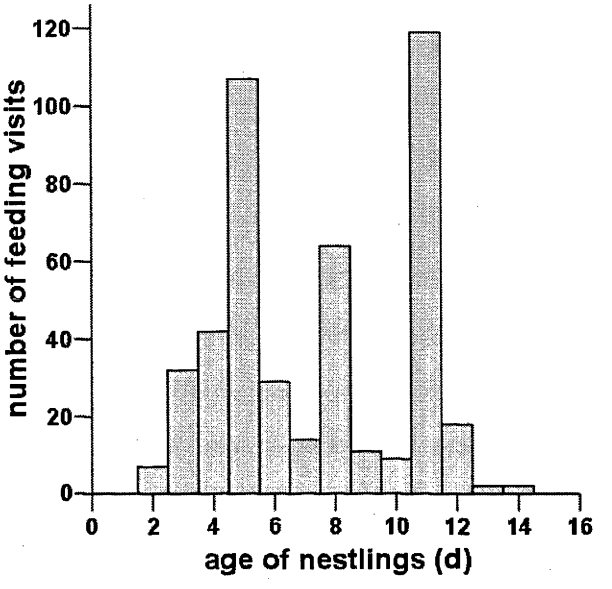


Figure 1: The number of recorded feeding visits according to nestling age. Mean fledge date is day 15.

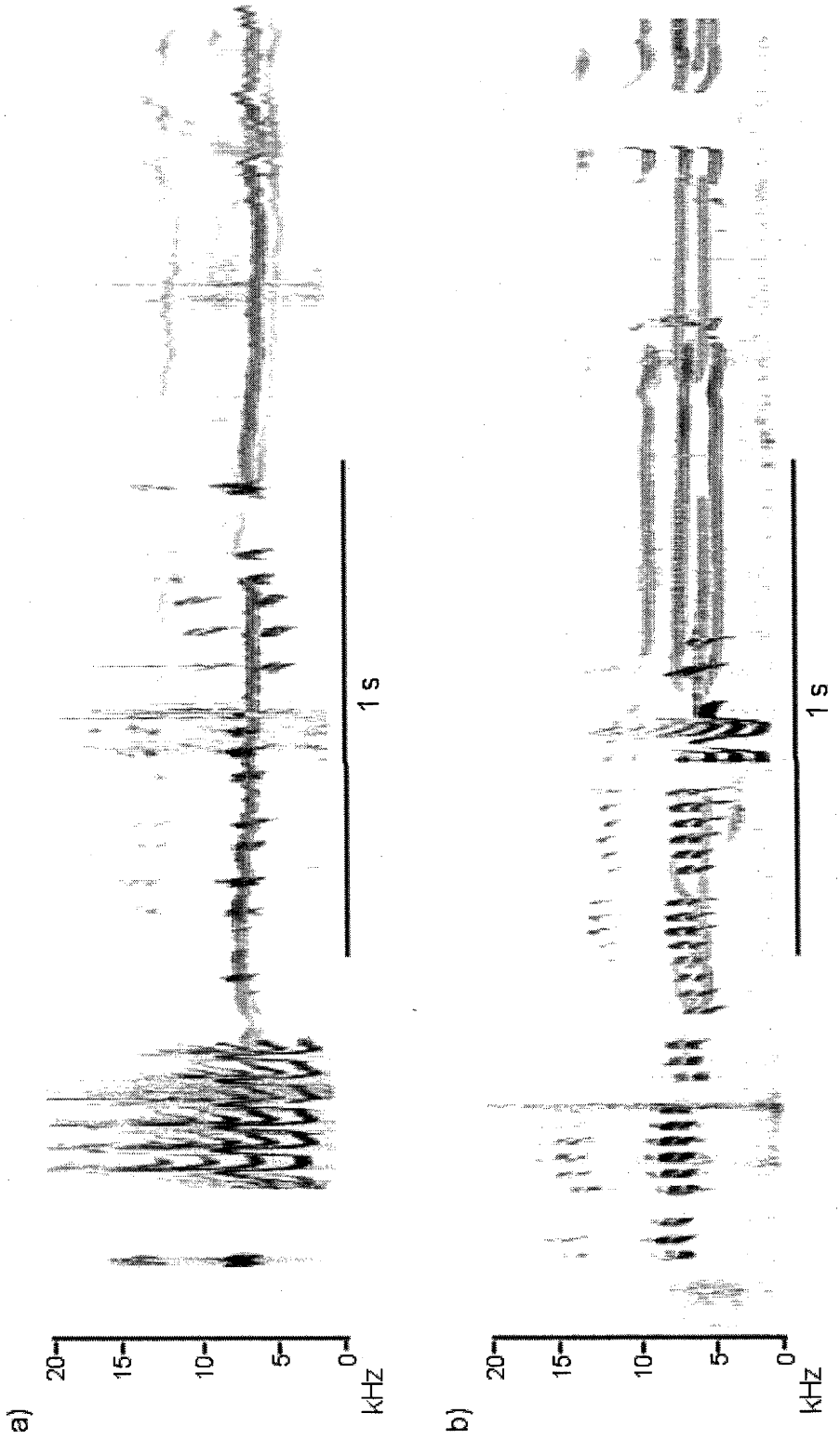


Figure 2: Two natural feeding visits with calling bouts comprising basic and complex call elements. The horizontal lines in the background are begging noises produced by (a) one and (b) two nestlings in response to the adult provisioning calls.

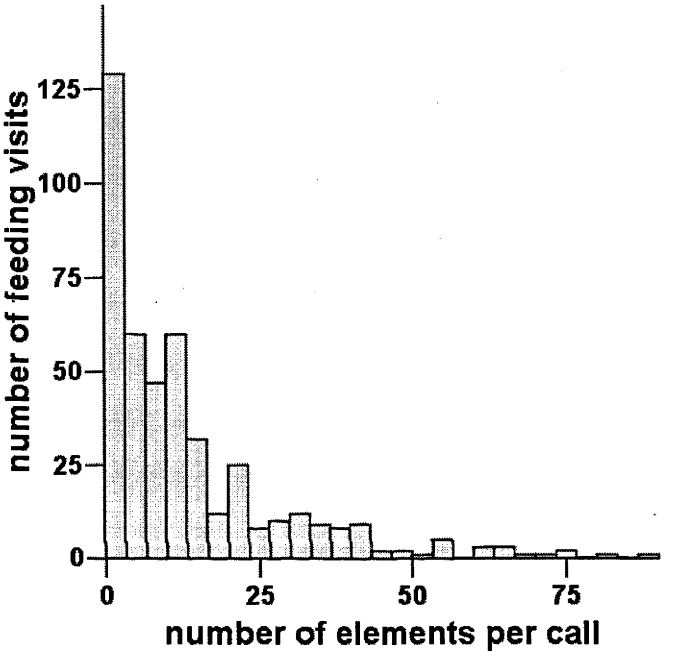


Figure 3: Distribution of the number of call elements that adults used during the recorded feeding visits. Extreme cases with more than 100 calls (n = 6, maximum 317) are not included.

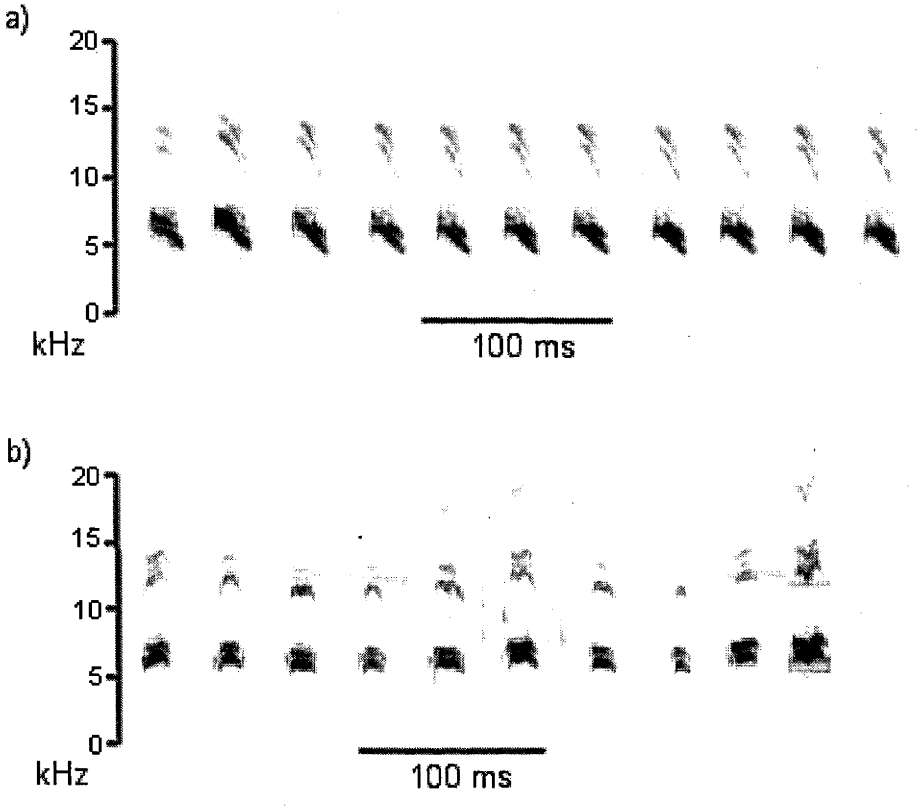
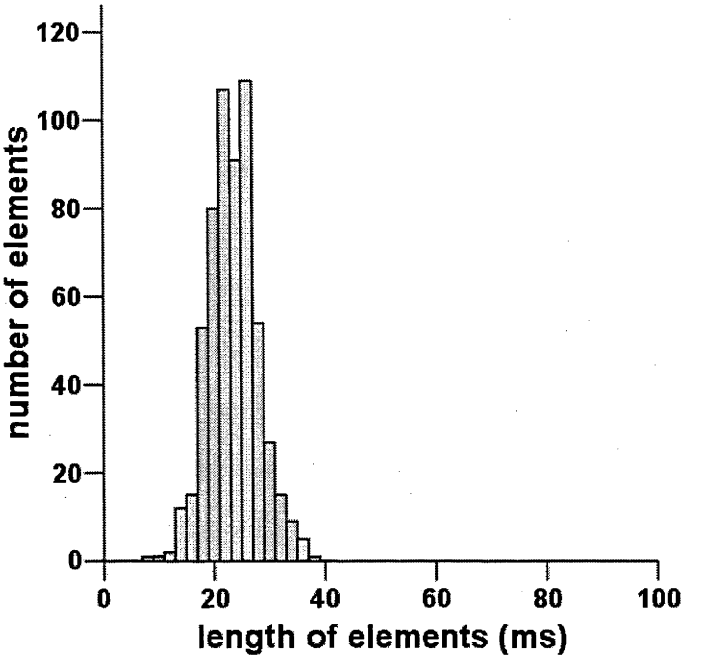


Figure 4: The two most common element types given during feeding visits that together constitute the vast majority of recorded provisioning elements. (a) The most common element type 'basic 1'; overall n = 4275. (b) The less common basic element type 'basic 2'; overall n = 457.

b)



(c)

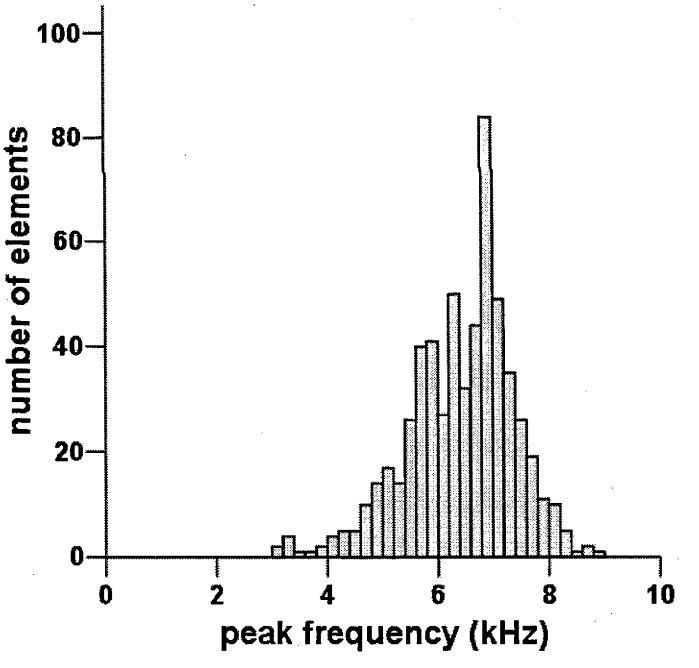
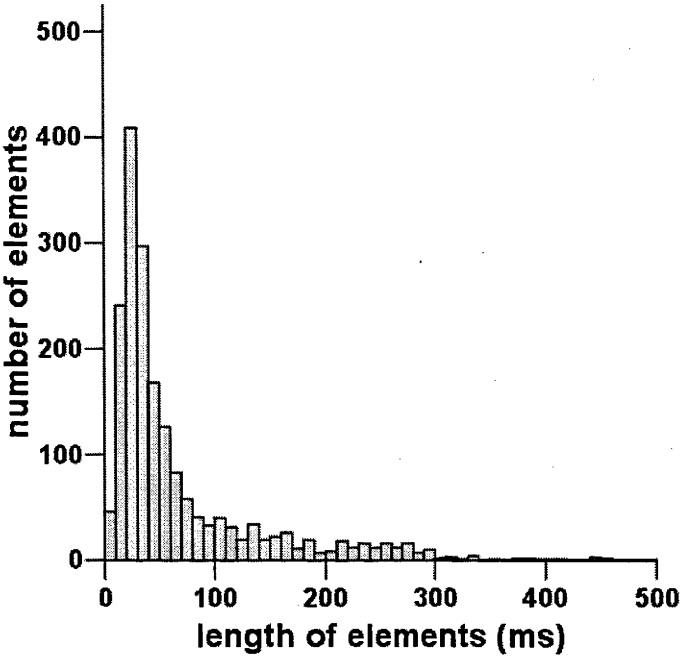


Figure 5: Basic call elements: (a) Distribution of element length and (b) distribution of peak frequencies. n = 582

b)



(c)

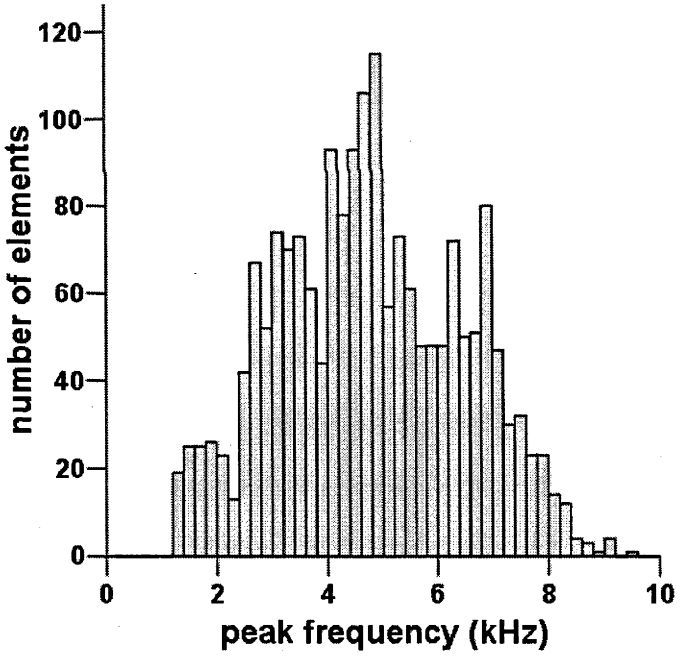


Figure 6: Complex call elements: (a) Distribution of element length. One element that was longer than 500 ms (645 ms) is not included. Note the 5 times longer time scale compared to the length distribution for basic elements (figure 5a). (b) Distribution of peak frequencies of all measured calls. n = 2353

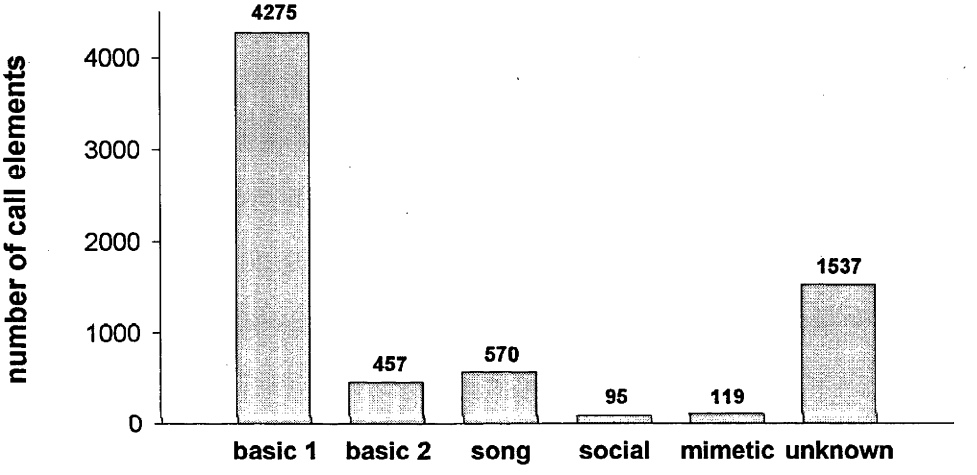


Figure 7: Distribution of recorded provisioning call elements over the identified groups of element types. Numbers above the bars give exact values. Calls that were given by brooding females when a male approached (see results) are not included because it is likely that they are not directed to the nestlings.

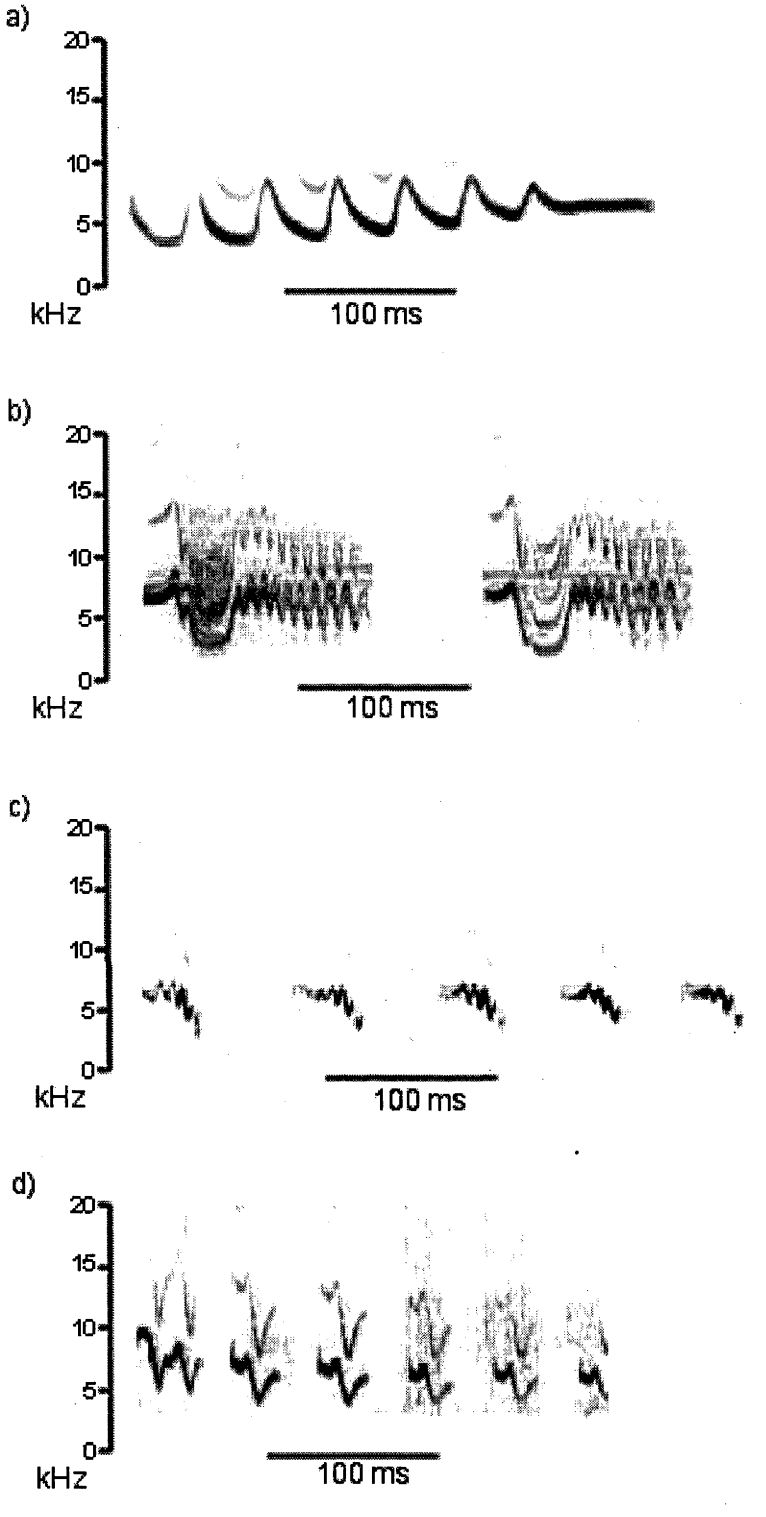


Figure 8: Four examples of provisioning call elements that have been identified as song elements sung by males from the study area during the 2003 season. (a, b) Song elements. (c, d) Introductory elements to songs. Note that in (d) only the second and third elements actually represent the type found as introduction to songs, while the other elements are variations of the same element.

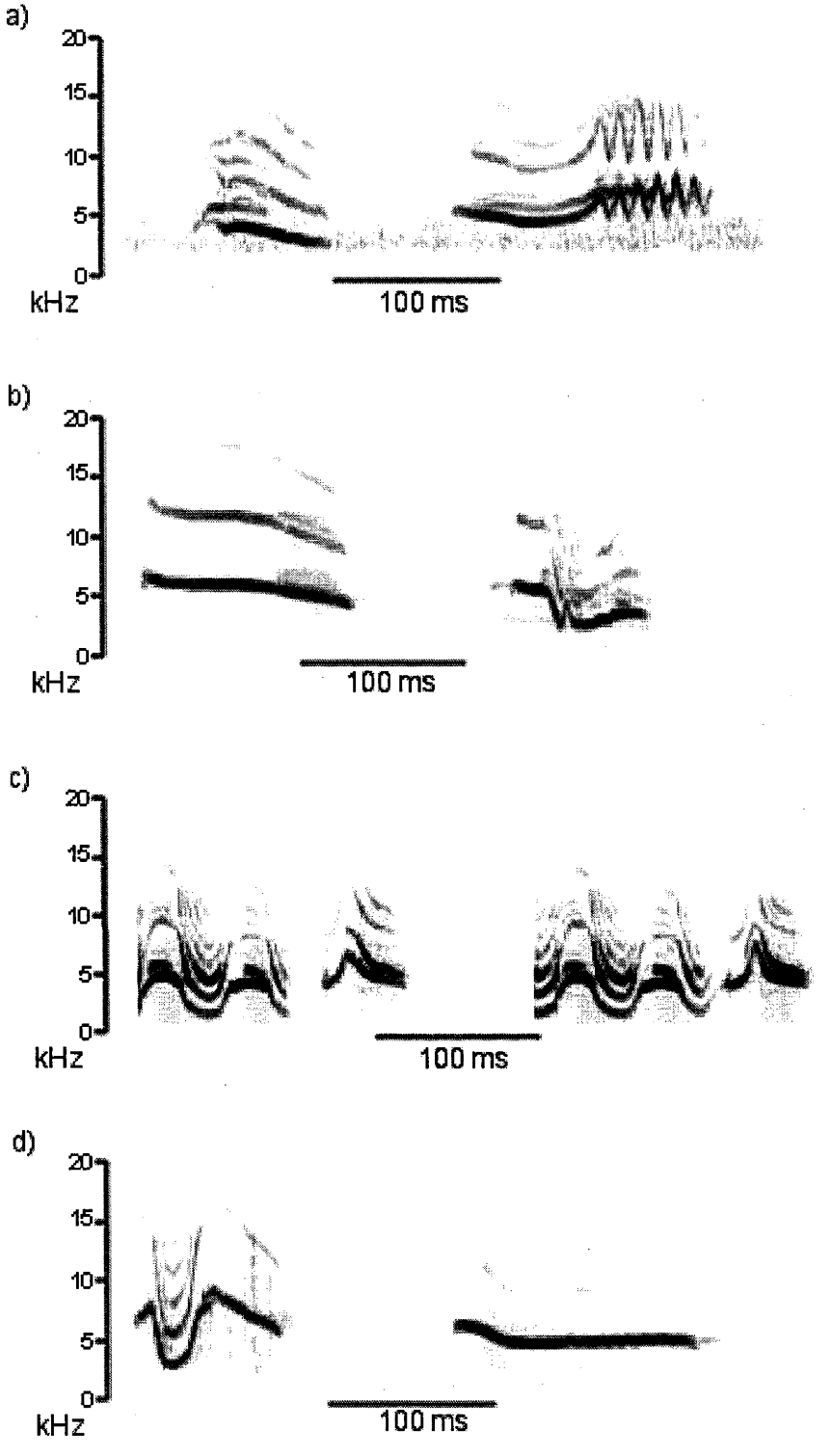


Figure 9: Potential song syllables that were given during feeding visits with several repetitions in a song-like manner. Except for (c) all spectrograms show one syllable. The first syllable elements in (a) and (b) and the second elements in (c) and (d) are not known song elements of the local population. The other elements have been found in songs. These combinations thus potentially represent previously undescribed song types of the study population.

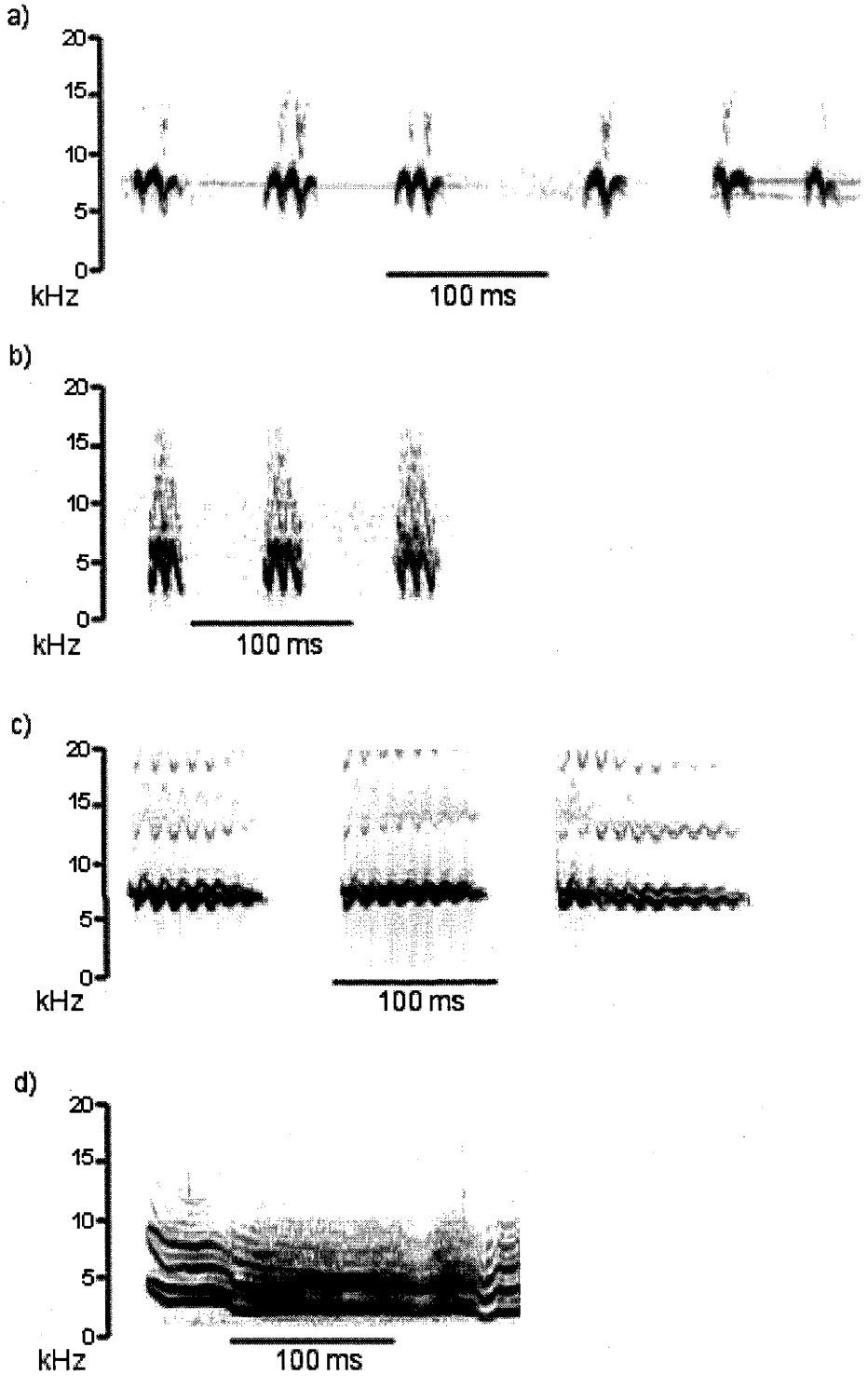


Figure 10: Provisioning call elements that have a structure similar to elements from other social contexts. (a) Elements similar to contact 'chips'. (b) Elements similar to pattern call elements. (c) Elements similar to aerial alarm 'trills'. (d) A call element that resembles a nestling begging 'whine'.

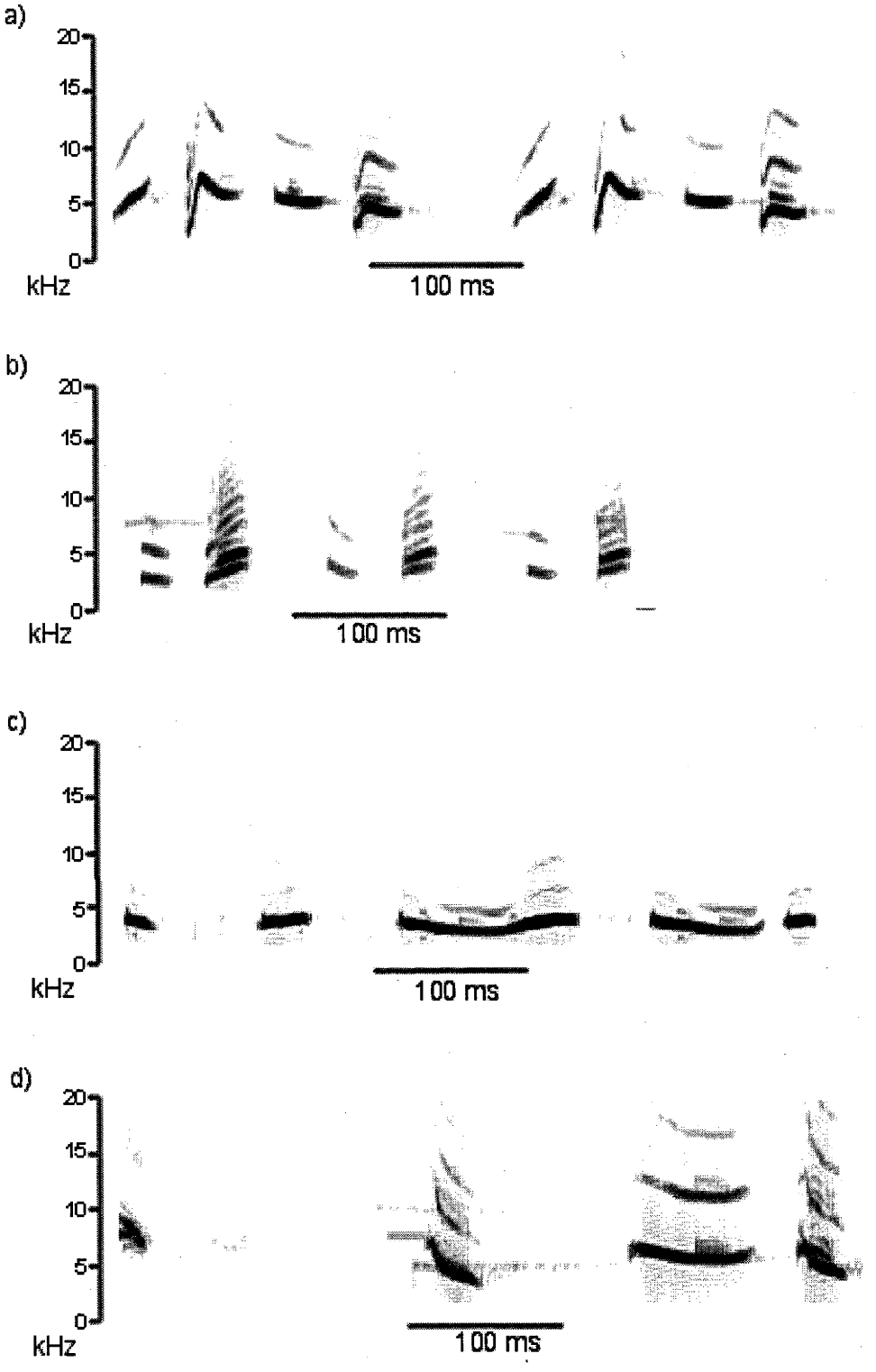


Figure 11: Imitation of other species. (a) The imitation of a yellow-rumped thornbill song. Two similar sequences are shown. (b) The imitation of a yellow-rumped thornbill call. (c) The imitation of a striated pardalote call. Both species occur in the study area. (d) A sequence that was repeated in exactly the same manner on two different occasions by the same bird. It is not a known scrubwren song pattern and represents a potential imitation of another species.

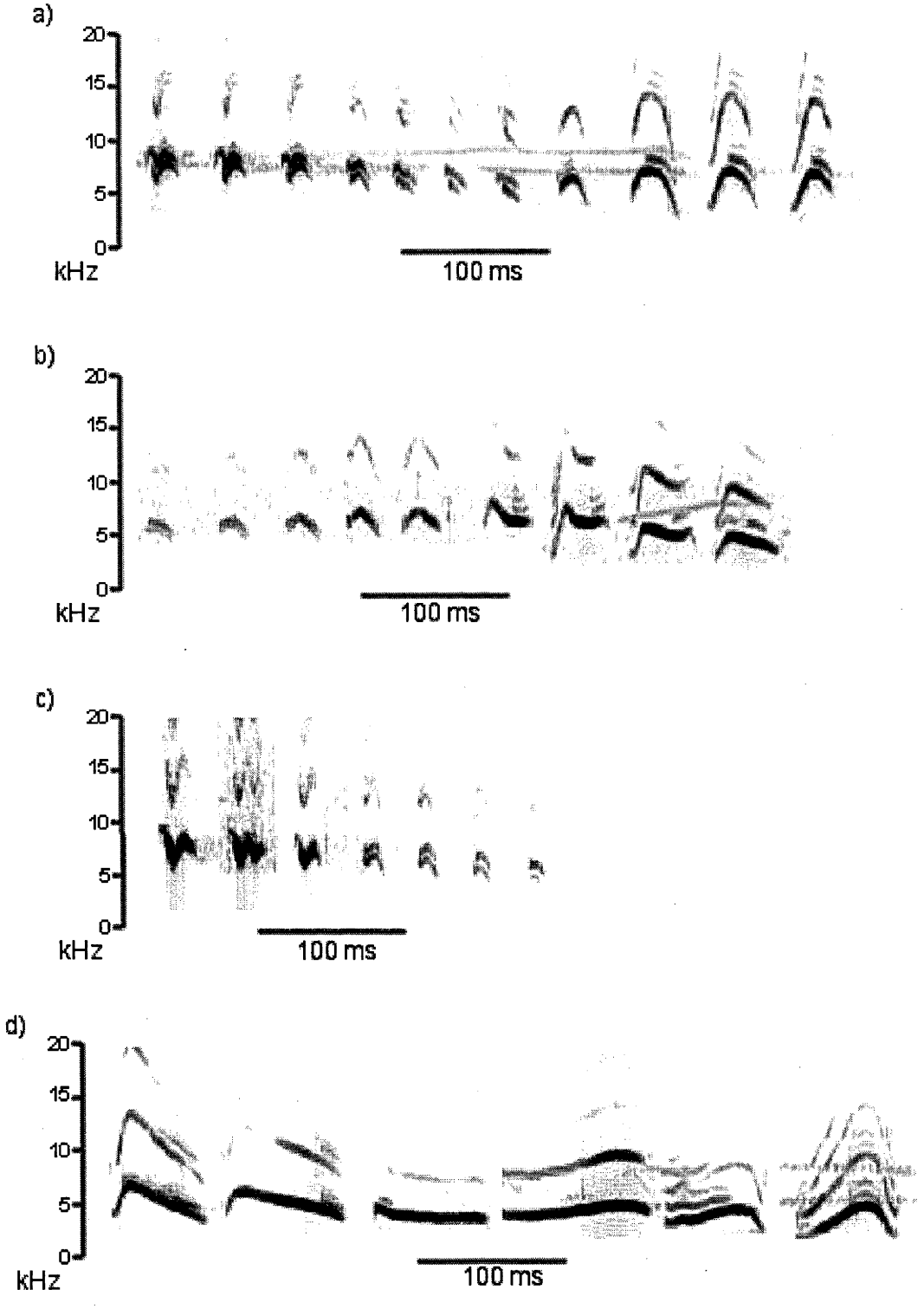


Figure 12: Changes from one element type to another with intermediate call elements. (a, b, c) These sequences were recorded during a single feeding visit and are displayed with the original inter-element distances. (d) This sequence was constructed from elements that were recorded during different feeding visits. Each element was produced by a different individual.

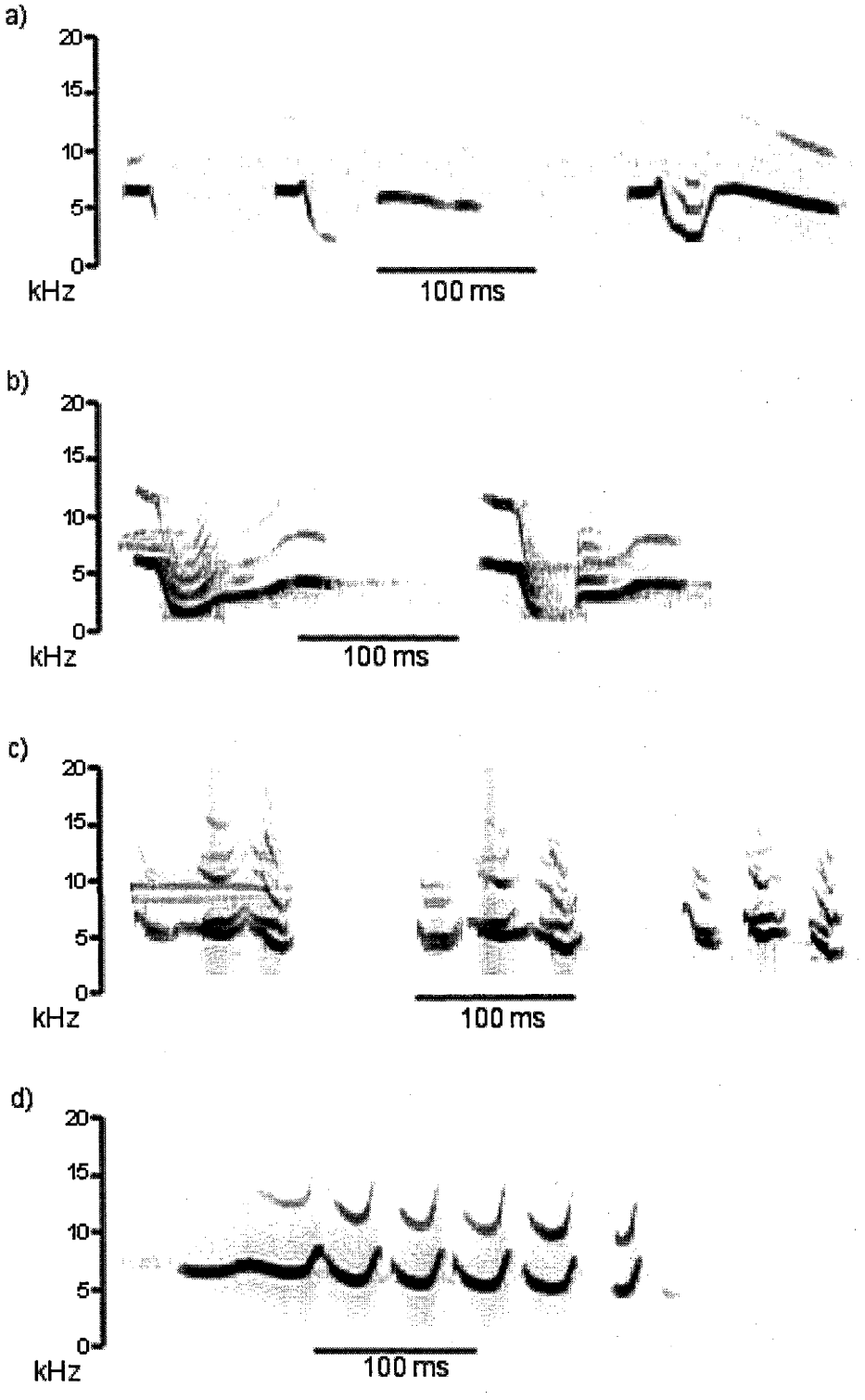


Figure 13: Fragmentation of element types. (a) All elements are displayed with the natural inter-element distances. (b) These two elements were given during one visit. (c) The first two elements were given during one visit while the same individual gave the last sequence the following day. (d) All inter-element distances are original.

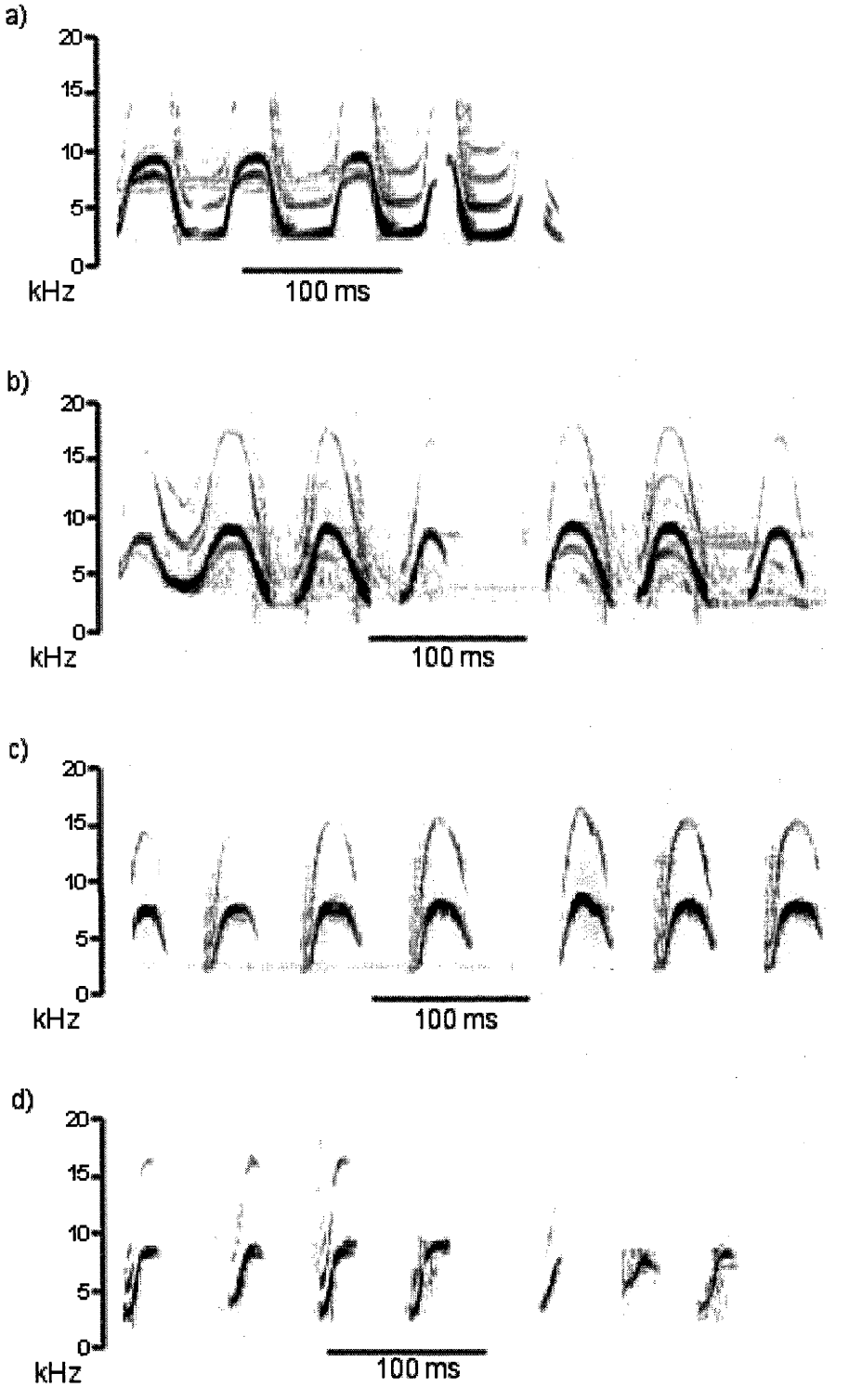


Figure 14: Fragmentation of element types. All elements within one spectrogram were given during one feeding visit. Elements in (c) and (d) are not displayed with the original inter-element distances.

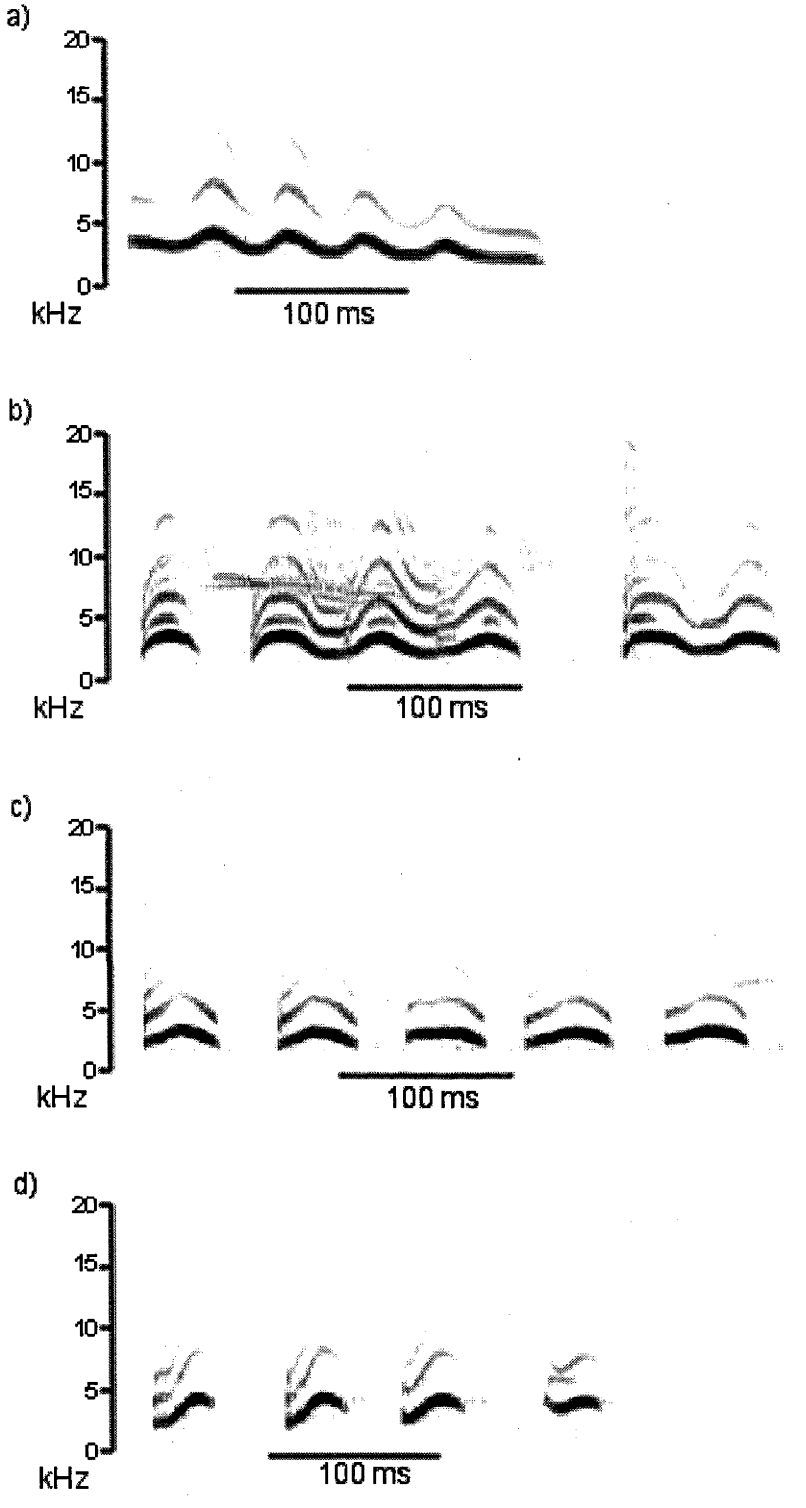


Figure 15: Fragmentation of element types. All elements within one spectrogram were given during one feeding visit. Elements in (d) are not displayed with the original inter-element distances.

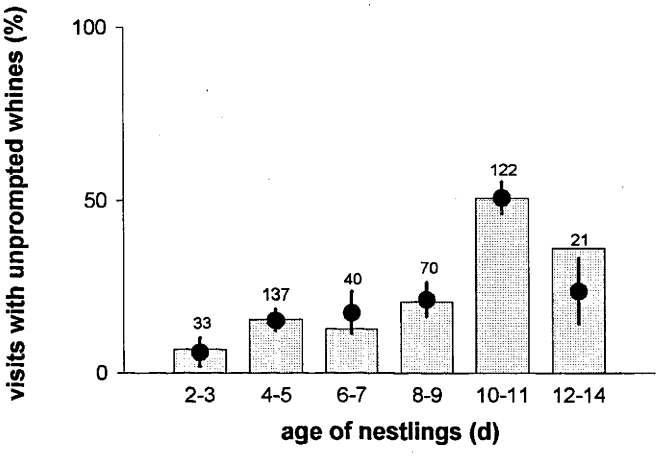
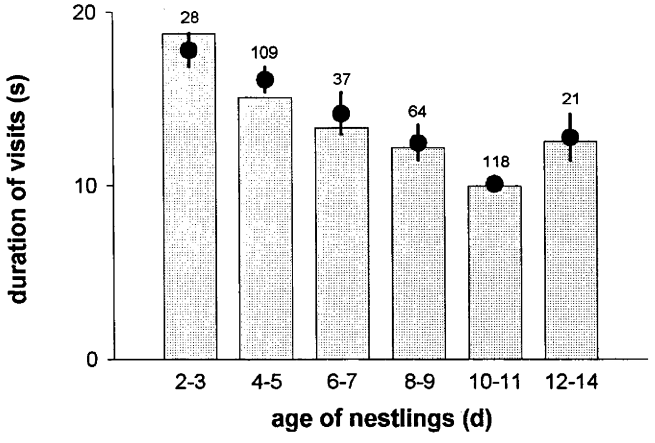


Figure 16: Proportion of nests at which nestlings responded to the approaching adult with whines before any provisioning calls were given. Bars show estimated means from a mixed model. Circles represent observed means with standard errors and sample sizes. Young fledge when they are about 15 days old.

a)



b)

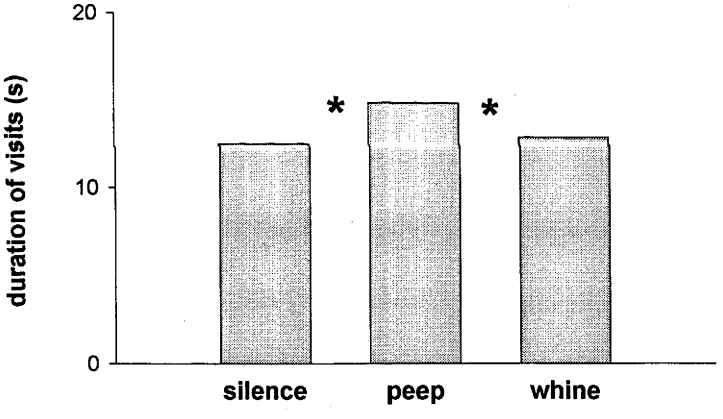
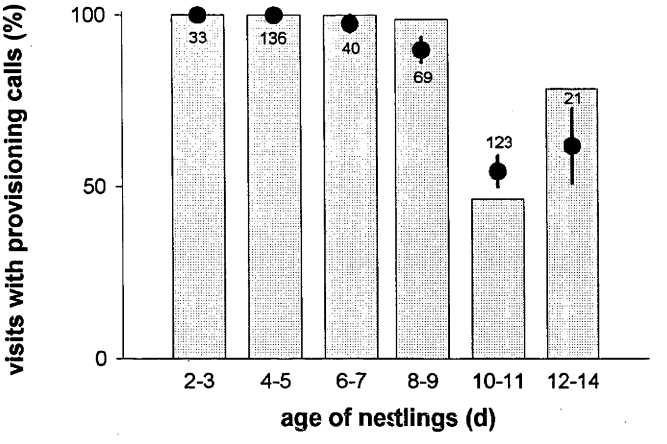


Figure 17: Duration of feeding visits. (a) Changes with the nestling age. Bars show estimated means from a mixed model. Circles represent observed means with standard errors and sample sizes. (b) Duration of feeding visits shown for nests where the nestlings' activity before a provisioning call was silence (n = 137), peeps (n = 133) or whines (n = 106). Bars represent estimated means from a mixed model. The stars indicate significant differences between factor levels.

a)



b)

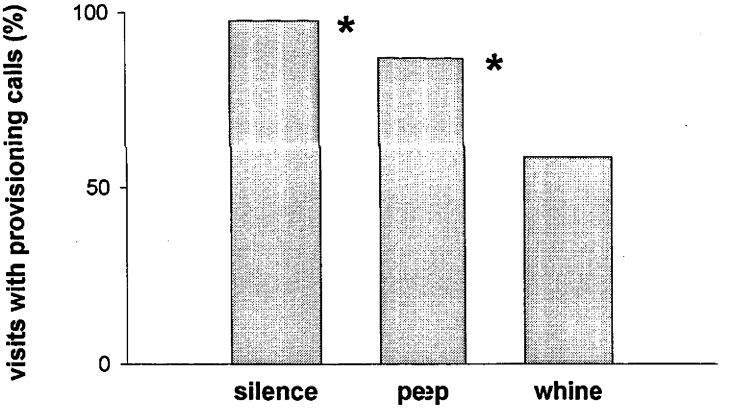
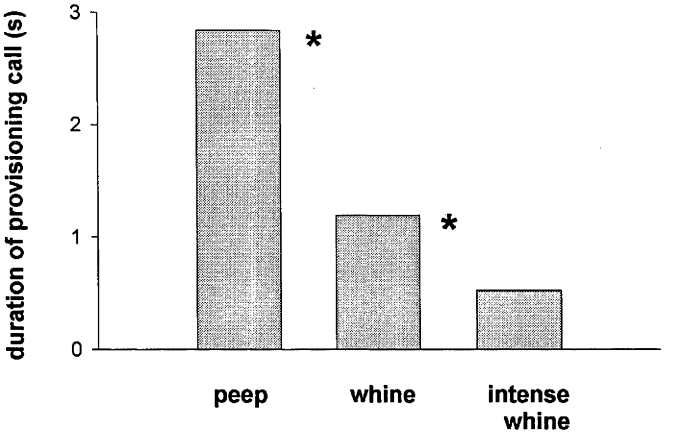


Figure 18: Proportion of nests at which provisioning calls were given. (a) Changes with nestling age. Bars show estimated means from a mixed model and circles represent observed means with standard errors and sample sizes. (b) Proportion of visits with provisioning calls shown for nests where the nestlings' activity before a provisioning call was silence (n = 163), peeps (n = 143) or whines (n = 112). Bars represent estimated means from a mixed model. The stars indicate significant differences between factor levels.

a)



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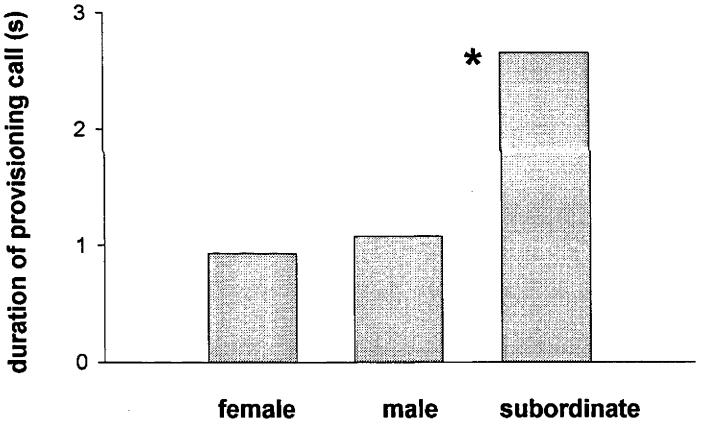


Figure 19: Length of provisioning calls. (a) Mean values for visits where nestlings responded to provisioning calls with peeps (n = 34), low intensity whines (n = 198) or high intensity whines (n = 82). (b) Mean values for females (n = 125), males (n = 170) and subordinates (n = 27). The bars represent estimated means from mixed models and the stars indicate a significant difference between factor levels.

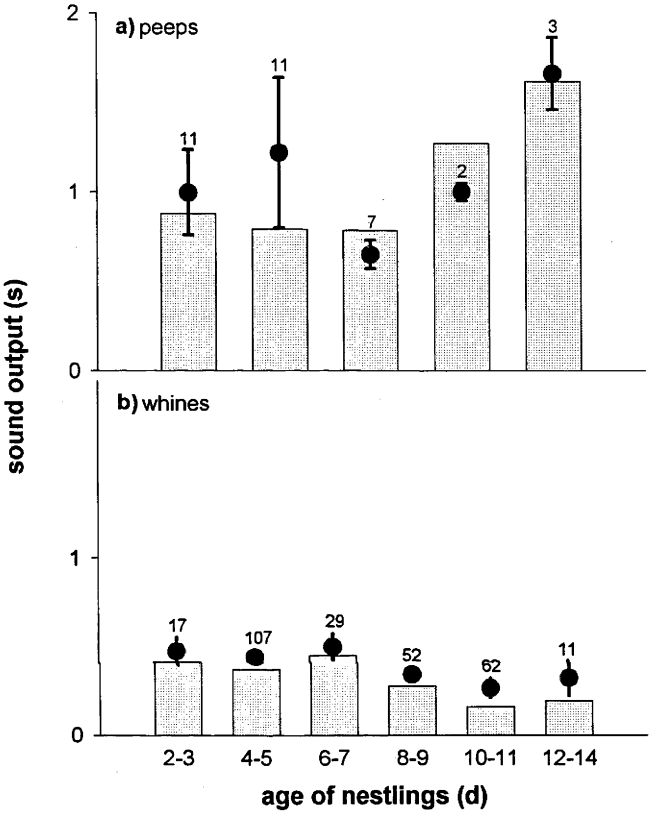


Figure 20: Sound output measured as the cumulative length of all elements of a provisioning call. Interaction between nestling age and nestling response. (a) Estimated and observed means for nests where nestlings responded with peeps. (b) Estimated and observed means for nests where nestlings responded with whines. Bars show estimated means from a mixed model and circles represent observed means with standard error.

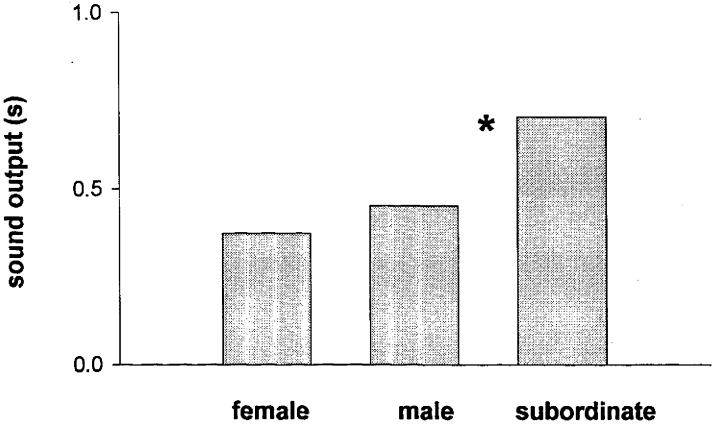
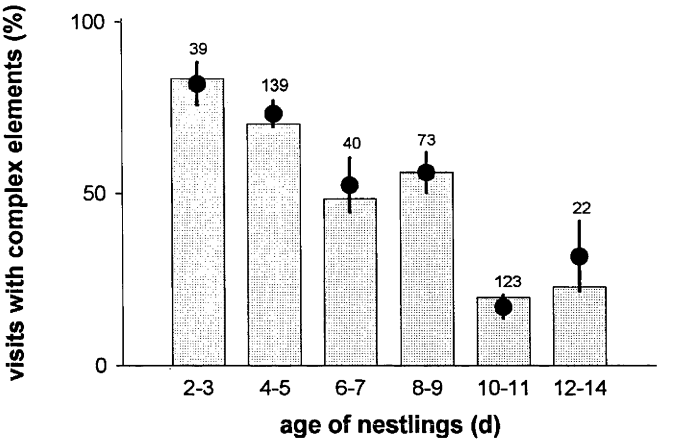


Figure 21: Sound output measured as the cumulative length of all elements of a provisioning call. Mean values for females (n = 125), males (n = 168) and subordinates (n = 27). The bars represent estimated means from a mixed model and the star indicates a significant difference.

a)



b)

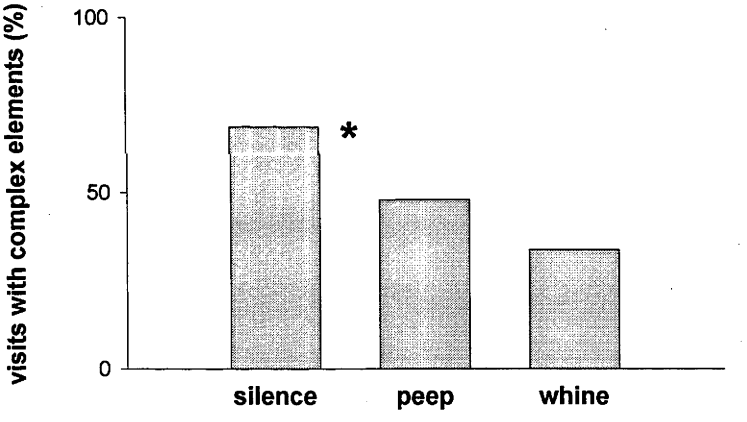


Figure 22: Proportion of visits where adults used complex provisioning call elements. (a) Changes with nestling age. Bars show estimated means from a mixed model and circles represent observed means with standard errors and sample sizes. (b) Proportion of visits with complex provisioning calls shown for nests where the nestlings' activity before a provisioning call was silence (n = 166), peeps (n = 144) or whines (n = 112). Bars represent estimated means from a mixed model. The star indicates a significant difference between factor levels.